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THE ADAPTIVE SIGNIFICANCE OF UV REFLECTANCE IN THE JUMPING SPIDER, COSMOPHASIS UMBRATICA (ARANEAE: SALTICIDAE)

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SUMMARY

Over the past few decades, the functional significance of ultraviolet-reflecting male ornaments has received much attention. Numerous theoretical and empirical studies have been conducted to explain the evolution of female mate choice, but data is often incomplete and research in invertebrates is limited. To date, the evolution of female mate choice still remains a controversial topic. Hence, my study set forth to examine the adaptive significance of ultraviolet reflectance and the ultimate causes of female mate choice, by using the jumping spider *Cosmophasis umbratica* as a study subject.

Cosmophasis umbratica is a jumping spider found in Singapore which exhibits extreme sexual dimorphism. These spiders are capable of seeing ultraviolet (UV) wavelengths but only adult males have UV-reflecting ornamentations which play an important role in female mate choice. A series of mate choice experiments were conducted to identify the UV-reflective characteristics which are important for making mate choice decisions by female *C. umbratica* spiders. Females exhibited a distinct preference for males with higher chroma and brightness in both UV and visible light (VIS) wavelengths. Preferred males were also found to have brighter carapaces and abdomens in the UVA and UVB wavelengths when compare to non-preferred males. This is the first demonstration that UV chroma and brightness are determinants of a male's mating success in this salticid species.

Experiments were also conducted to examine the fitness consequences of this UV-based female mate choice. Preferred and non-preferred males were mated with females, and the development of their offspring was monitored. Females do not receive direct benefits in terms of fertility as a result of their mate choice. Nonetheless, females which mated with preferred males were found to produce offspring with higher survivorship, shorter development time, larger size, and higher attractiveness. This study is the first to demonstrate that chosen males confer higher performance on their offspring, allowing female *C. umbratica* spiders to enjoy indirect genetic benefits.

I also investigated whether UV reflectance is condition-dependent, by monitoring the development of *C. umbratica* reared on diets of different nutritional contents. Spiders reared on a nutrient-enriched diet had shorter development time, larger body size and the males had higher chroma and brightness in both UV and VIS wavebands. These findings showed that UV reflectance is dependent on the diet quality of *C. umbratica* during its development. Additionally, UV reflectance is positively correlated to fitness components such as development time and size. Therefore, these findings indicate that UV reflectance is a reliable indicator of male quality in this species. This is consistent with the good genes hypothesis which predicts that females gain indirect genetic benefits as a result of their mate choice.

In conclusion, the findings in this thesis support the hypotheses that UV-reflecting ornamentations in *C. umbratica* play important roles in female mate choice by functioning as reliable indicators of male quality, and choosy females gain indirect genetic benefits.

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CHAPTER 1

General Introduction

Ultraviolet vision

Humans can perceive light in the wavelength range of 400 to 700 nm, which is commonly known as the human-visible light range, but ultraviolet (UV) wavelengths below 400 nm are visible to many other animals. Many animals have been shown to be capable of seeing UV wavelengths, particularly vertebrates (Shi *et al.* 2001; Shi & Yokoyama 2003) such as birds (Bennett & Cuthill 1994; Chen *et al.* 1984; Cuthill *et al.* 2000a, b; Rajchard 2009; Smith *et al.* 2002a), fish (Archer & Lythgoe 1990; Bennett *et al.* 1996; Bowmaker & Kunz 1987; Bowmaker *et al.* 1991; Losey *et al.* 1999; McFarland & Loew 1994; Sieback *et al.* 2010; Smith *et al.* 2002b), reptiles (Ammermuller *et al.* 1998; Ellingson *et al.* 1995; Fleishman *et al.* 1993), and a few species of mammals (Jacobs & Deegan 1994; Jacobs *et al.* 1991; Winter *et al.* 2003). UV vision has also been found in invertebrates (Salcedo *et al.* 2003), particularly in insects (Briscoe & Chittka 2001; Kemp et al. 2008), crustaceans (Cronin *et al.* 1994; Frank & Widder 1996; Goldsmith & Cronin 1993; Smith & Macagno 1990), and spiders (Blest *et al.* 1981; DeVoe 1975; Land 1969b; Peaslee & Wilson 1989; Yamashita & Tateda 1976).

Some functions of UV vision involve regulation of circadian rhythms, navigation, foraging, and intraspecific communication (Tovée 1995). It has been shown that UV vision plays a role in the regulation of circadian rhythms in animals such as

canaries, golden hamsters and rats (Bernard & Remington 1991; Brainard *et al.* 1994; Tovée 1995). For some insects such as the honeybee and desert ant (Wehner 1989), fishes such as the trout (Hawryshyn & Bolger 1990) and some species of birds (Coemans *et al.* 1994), it has been proposed that UV vision plays an important role in navigation. Various animals have also been found to use UV vision in foraging. When exposed to sunlight, flowers and fruits scatter and reflect UV wavelengths whereas the leaves, bark, and soil do not (Endler 1993). Hence, flowers and fruits are likely to be more distinguishable to animals with UV vision. In fact, many birds and insects depend on UV vision to forage for fruits and nectar-rich flowers (Chittka *et al.* 1994; Goldsmith 1980; Menzel & Shmida 1993; Siitari *et al*. 1999). It has also been proposed that many predatory birds, reptiles and arthropods use UV vision to detect their UV-reflecting prey (Church *et al.* 1998; Honkavaara *et al.* 2002; Li & Lim 2005; Oxford & Gillespie 1998; Siitari *et al.* 2002b; Vane-Wright & Boppre 1993; Viitala *et al.* 1995).

Numerous studies have also provided evidence for the role of UV vision and UV reflectance in intraspecific communication (Bennett & Cuthill 1994; Briscoe & Chittka 2001; Cuthill *et al.* 2000a, b; Jacobs 1992; Tovée 1995), particularly in vertebrates such as birds (Alonso-Alvarez *et al.* 2004; Andersson & Amundsen 1997; Andersson *et al.* 1998; Bennett *et al.* 1996, 1997; Hunt *et al.* 1997, 1998, 1999; Johnsen *et al.* 1998; Maddocks *et al.* 2001; Maier 1993; Pearn *et al.* 2001; Siefferman & Hill 2005; Siitari *et al.* 2002a; Zampiga *et al*. 2008), fish (Boulcott *et al.* 2005; Kodric-Brown & Johnson 2002; Rick *et al.* 2006; Smith *et al.* 2002a; White *et al.* 2003), and reptiles (Fleishman *et al.* 1993; Stapley & Whiting 2006; Whiting *et al.* 2006). Comparatively, research in invertebrates is limited (Brunton

& Majerus 1995; Kemp *et al.* 2008; Li *et al.* 2008b; Lim *et al.* 2007, 2008; Robertson & Monterio 2005).

Ultraviolet vision and reflectance in jumping spiders

Spiders of the family Salticidae (jumping spiders) are known to possess excellent colour vision (Nakamura & Yamashita 2000). Their remarkable vision is believed to enhance behaviours such as hunting, courtship displays and other visual communication (Crane 1949a, b; Forster 1982; Jackson & Blest 1982; Li & Jackson 1996; Peckham & Peckham 1889, 1890, 1894). Their large, principal eyes (i.e. anterior median eyes) contain photoreceptors that are sensitive to human-visible wavelengths (400-700 nm) as well as UV wavelengths (Blest *et al.* 1981; DeVoe 1975; Land 1969b; Peaslee & Wilson 1989; Yamashita & Tateda 1976).

Many salticids are brightly coloured, and some salticids are also iridescent, a characteristic which is attributed to their cuticular scales (Hill 1979; Townsend & Felgenhauer 1998a, b, 1999). It is also known that some salticids have various body parts reflecting UV light (Li *et al.* 2008a; Lim & Li 2006b; Lim *et al.* 2007). Behavioural evidence has shown that salticids are sensitive to UV reflectance, and use UV-reflecting body parts in intraspecific communication, particularly in female mate choice (Li *et al.* 2008b; Lim & Li 2006a; Lim *et al*. 2008). However, the adaptive significance of UV-based female mate choice in salticids is unclear.

Evolution of female mate choice and male ornaments

Female mate choice for ornamented males has been of particular interest to many researchers in the past thirty years. Numerous theoretical and empirical studies have been conducted to explain the origins and maintenance of female mate choice, and several mechanisms have since been proposed (Andersson 1994; Jones & Ratterman 2009; Kokko *et al.* 2003, 2006; Majerus 1986; Møller & Jennions 2001). However, empirical data on the evolution of female mate choice is often incomplete and controversial (e.g. Arnqvist & Rowe 2005; Cameron *et al*. 2003; Cordero & Eberhard 2003; Kokko *et al*. 2003, 2006). Currently, there are several models for the evolution of female mate choice, such as the direct benefits models and indirect benefits models, including the Fisherian sexy son and good genes models (Andersson 1994; Andersson & Simmons 2006; Fisher 1915, 1930; Hamilton & Zuk 1982; Kirkpatrick 1982; Kokko *et al.* 2003; Kotiaho & Puurtinen 2007; Lande 1981; Mead & Arnold 2004; Møller & Jennions 2001; Pomiankowski 1987; Weatherhead & Robertson 1979; Zahavi 1975).

The direct benefits models predict that females choose mates that provide immediate benefits such as nuptial gifts (e.g. spermatophores of male bushcrickets; Gwynne 1984), parental care (e.g. blackbirds and sticklebacks; Preault *et al. 2005*; Ostlund & Ahnesjo 1998), protection (e.g. elephant seals and dung flies; Galimberti *et al.* 2000; Borgia 1981), parasite avoidance (e.g. grain beetles; Worden & Parker 2005), and increased fecundity or fertility (e.g. lemon tetras and fruit flies; Nakatsuru & Kramer 1982; Markow *et al.* 1978). The evolution of female mate choice in species where males provide no immediate

benefits to females is explained by the indirect benefits models. According to the good genes model, the male's ornament is an condition-dependent indicator of his genetic quality (Zahavi 1975), and thus the female gains indirect genetic benefits in the form of increased offspring viability (e.g. ambush bugs and bank voles; Lopuch & Radwan 2009; Mead & Arnold 2004; Moore 1994; Pomiankowski 1988; Punzalan *et al.* 2008). Based on the Fisherian sexy son model, an initial arbitrary female preference results in a genetic correlation between the ornament and preference genes in which the ornament gene is selected for together with the preference gene (e.g. sandflies; Jones *et al.*1998; Kirkpatrick 1982; Lande 1981). Over time, self-reinforcement loops lead to the development of greater preference and more pronounced traits, until the survival costs of bearing the trait counterbalance the reproductive benefits of possessing it (Fisher 1915, 1930). Females benefit because when they mate with attractive males, they will produce attractive sons that are similarly favoured by females (Weatherhead & Robertson 1979).

In addition to the direct and indirect benefits models, there is also the sensory exploitation model which predicts that male ornaments evolved to take advantage of pre-existing sensory-bias in females (Fleishman 1992; Ryan 1998; Smith *et al.* 2004). Finally, there are the models of genetic compatibility which suggest that females prefer to mate with males that are genetically compatible with them (Neff & Pitcher 2005; Ryan & Altmann 2001; Tregenza & Wedell 2000; Zeh & Zeh 1996), and sexual conflict which involves antagonistic seduction and resistance between the two sexes (Cameron *et al.* 2003; Holland & Rice 1998; Maan & Taborsky 2008; Parker 2006).

UV-based female mate choice in *Cosmophasis umbratica*

Over the past two decades, the functional significance of UV-reflecting male ornaments has received much attention, particularly in vertebrates such as birds (Andersson & Amundsen 1997; Andersson *et al.* 1998; Bennett *et al.* 1996, 1997; Hunt *et al.* 1997, 1998, 1999; Johnsen *et al.* 1998; Maddocks *et al.* 2001; Maier 1993; Pearn *et al.* 2001; Siitari *et al.* 2002a), fishes (Garcia & Perera 2002; Kodric-Brown & Johnson 2002; Rick *et al.* 2006; Smith *et al.* 2002; White *et al.* 2003), and reptiles (Fleishman *et al.* 1993). Comparatively, such research in invertebrates is scarce (Brunton & Majerus 1995; Li *et al.* 2008; Lim *et al.* 2007, 2008; Robertson & Monterio 2005).

Cosmophasis umbratica is a jumping spider found in Singapore that exhibits sexual colour dimorphism. Males have iridescent markings on the cephalothorax (also known as carapace) and a silvery-white stripe along the dorsal surface of a black abdomen (Figure 1-1a), while females are usually green on the cephalothorax and have a mixture of brown and black on the abdomen (Figure 1-1b). It is known to be capable of seeing UV wavelengths, but only adult males have UV-reflecting ornaments (Lim & Li 2006a, 2006b; Lim *et al.* 2007). Many studies have also shown that such male UV-reflecting ornaments function in the context of sexual selection (e.g. Alonso-Alvarez *et al.* 2004, Cuthill *et al.* 2000, and Siefferman and Hill 2005). In fact, a recent study revealed that *C. umbratica* females prefer UV-reflecting males over UV-lacking males (Lim *et al.* 2008), hence providing evidence for the importance of UV reflectance in female mate choice. However, whether females show a preference for males with specific UV-reflective traits has not been empirically tested. Hence, the first part of my

research aimed to test whether *C. umbratica* females use UV-reflective traits of males in making mate choice decisions.

In salticids such as *C. umbratica*, males generally do not provide females with material (i.e. direct) benefits such as nuptial gifts and parental care. However, it is possible that mating with preferred males may provide females with other forms of direct benefits such as increased fecundity or fertility (reviewed in Møller & Jennions 2001). It is also possible that preferred males have nothing more to offer to females other than good genes. Currently, nothing is known about the evolution of UV-based female mate choice in *C. umbratica*. Hence, the objective of the second part of my research is to determine the fitness consequences of UV-based female mate choice in *C. umbratica*.

Several studies have revealed that UV-based male ornaments are correlated with male quality in many animals, such as in the Blue-Black Grassquits *Volatinia jacarina* (see Doucet 2002), the blue tits *Parus caeruleus* (see Peters *et al.* 2006), the red grouse *Lagopus lagopus scoticus* (see Mougeot *et al.* 2005), the orange sulphur butterfly *Colia eurytheme* (see Kemp 2006), and others (Delhey *et al.* 2006; Doucet *et al.* 2005, 2006; Keyser & Hill 1999, 2000). Recently, a study on *C. umbratica* has demonstrated that UV reflectance is indicative of male age and body conditions, hence suggesting that UV reflectance is condition-dependent in *C. umbratica* (see Lim & Li 2007). These findings suggest that UV signals carry specific information which may serve as a criterion used by females when making mate choice decisions, perhaps by indicating male quality. However, no study has been conducted to examine the dietary effects on UV reflectance.

Hence, the final part of my research focused on investigating whether UV reflectance is dependent on nutritional quality. In order to understand its implications for sexual selection theory, dietary effects on fitness of *C. umbratica* juveniles were also examined.

In summary, the three main research questions of this study are:

1. What male UV-reflective characteristics are important to *C. umbratica* females in making mate choice decisions?
2. What are the fitness consequences of UV-based female mate choice in *C. umbratica*?
3. What are the effects of diet quality on UV reflectance and fitness of *C. umbratica*?

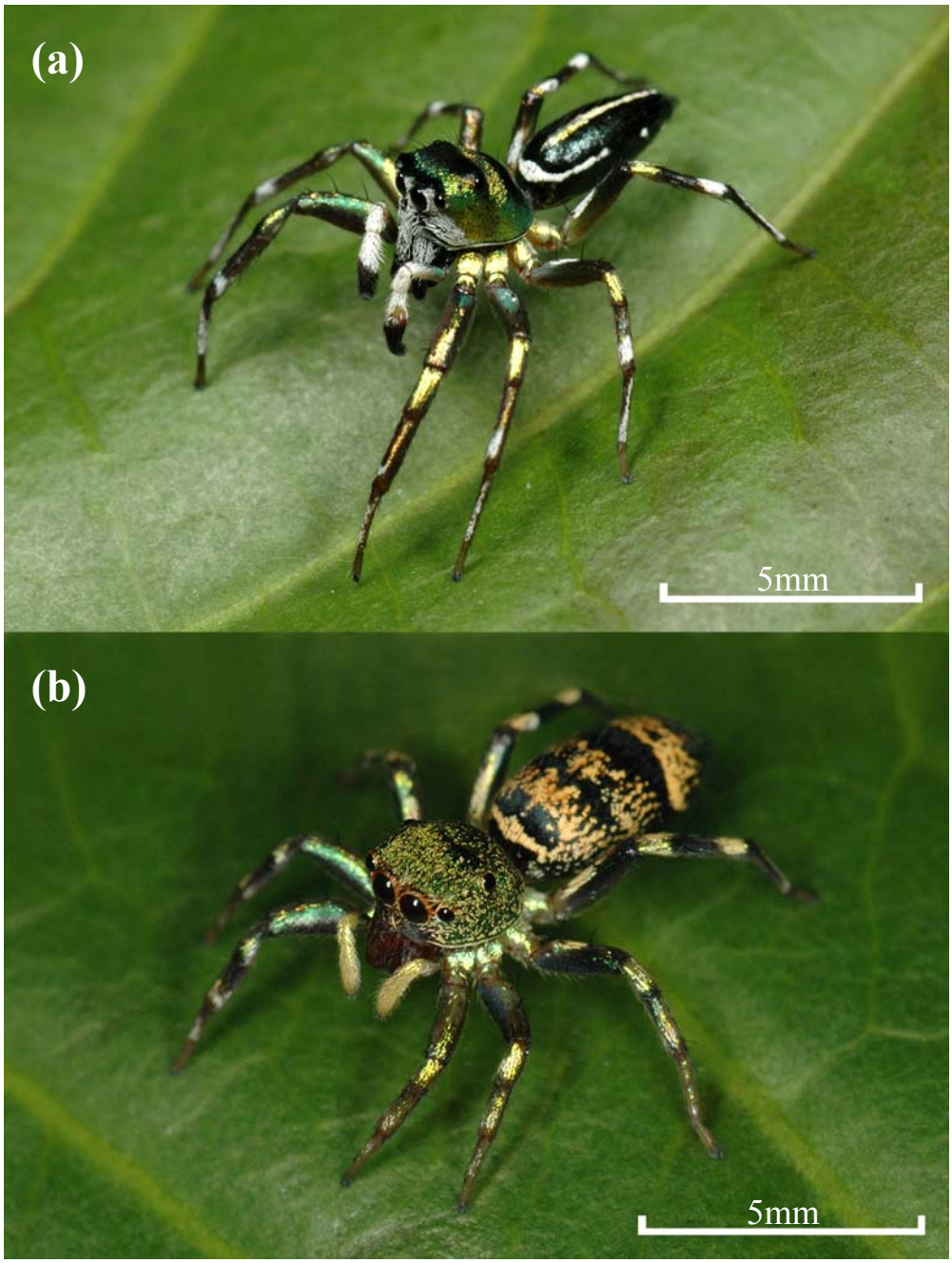

Figure 1-1. Jumping spider *Cosmophasis umbratica* showing sexual dimorphism in colour and size. (a) Adult male; and (b) adult female.

CHAPTER 2

Females Prefer Males with Brighter and More Saturated UV Reflectance in the Jumping Spider *Cosmophasis umbratica*

Abstract. Numerous studies have shown that UV reflectance of male ornaments plays an important role in determining the bearer's mating success. The sexual dimorphic jumping spider *Cosmophasis umbratica* is known to be capable of seeing UV light, but only the adult males bear UV-reflecting ornaments which are known to be signals used by females in making mate choice decisions. However, the reflectance spectral characteristics that are important in female mate choice have yet to be identified. In this study, a series of mate choice experiments were performed to identify the UV-reflective characteristics that serve as criteria used by *C. umbratica* females when making mate choice decisions. Females exhibited a distinct preference for males with higher chroma and brightness in both UV and visible (VIS) wavelengths. Preferred males were also found to have brighter carapaces and abdomens in the UVA and UVB wavelengths when compared to non-preferred males. This is the first demonstration that UV chroma and brightness may be reliable indicators of a male's mating success in this salticid species.

Keywords: Jumping spider, *Cosmophasis umbratica*, ultraviolet light, sexual selection, female mate choice.

INTRODUCTION

Ultraviolet (UV) vision has been well studied in many animals, particularly its role in intraspecific communication (Bennett & Cuthill 1994; Briscoe & Chittka 2001; Cuthill *et al.* 2000a, b; Jacobs 1992; Tovée 1995). Many animals also possess body parts that reflect UV light, and it is interesting to note that in species that exhibit sexual dimorphism, UV-reflecting ornaments are commonly involved in intraspecific interactions. Therefore, it is thought that the evolution of such traits might be the consequence of sexual selection (Cuthill *et al.* 2000a, b; Li *et al.* 2008b; Lim & Li 2008; Siitari *et al.* 2002a).

Over the past two decades, the functional significance of UV-reflecting male ornaments has received much attention, particularly its role in female mate choice in a variety of vertebrates such as birds (Andersson & Amundsen 1997; Andersson *et al.* 1998; Bennett *et al.* 1996, 1997; Hunt *et al.* 1997, 1998, 1999; Johnsen *et al.* 1998; Maddocks *et al.* 2001; Maier 1993; Pearn *et al.* 2001; Siitari *et al.* 2002a), fishes (Garcia & Perera 2002; Kodric-Brown & Johnson 2002; Rick *et al.* 2006; Smith *et al.* 2002; White *et al.* 2003), and reptiles (Fleishman *et al.* 1993). Comparatively, such research in invertebrates is limited (Brunton & Majerus 1995; Li *et al.* 2008b; Lim *et al.* 2007, 2008; Robertson & Monterio 2005).

Salticids have excellent vision and are capable of seeing UV wavelengths (Blest *et al.* 1981, 1990; Devoe 1975; Land 1969a, b, 1985; Nakamura & Yamashita 2000; Peaslee & Wilson 1989; Yamashita & Tateda 1976). *Cosmophasis*

umbratica (Araneae: Salticidae) is a jumping spider found in Singapore that exhibits extreme UV sexual colour dimorphism: only adult *C. umbratica* males have structural-based UV-reflecting ornaments while females lack such characteristics (Land *et al*. 2007; Lim & Li 2006a, 2006b; Lim *et al.* 2007). Behavioural evidence has shown that UV reflectance is important in intraspecific interactions in this species. For instance, in male-male interactions, UV reflectance may have a role in indicating the resource holding potential (RHP) of *C. umbratica* adult males (Lim, 2006). Studies have also shown that UV reflectance is indicative of male age and body conditions, thus demonstrating that UV reflectance in *C. umbratica* is condition-dependent (Lim & Li 2007). These findings suggest that UV signals carry specific information, and may have a role in female mate choice. In fact, a recent study revealed that *C. umbratica* adult females spent more time observing the courtship displays of UV-reflecting males rather than those whose UV reflectance was blocked by UV-blocking filters (Lim *et al.* 2008), hence providing evidence for the function of UV reflectance in female mate choice. Therefore, it is possible that UV signals serve as a criterion used by females when making mate choice decisions, perhaps by indicating male quality. However, the specific UV-reflective characteristics that are important for this role are currently unknown. Hence, this study attempted to identify the UV-reflective characteristics that are important for making mate choice decisions by female *C. umbratica* spiders.

MATERIALS AND METHODS

Spider collection and maintenance

All *Cosmophasis umbratica* spiders were collected as juveniles or sub-adults (one more moult before becoming adults) from Ulu Pandan Park Connector in Singapore during the day (particularly at 0900-1100hrs, and 1600-1800hrs) between June and December in 2008. *C. umbratica* is commonly found on the leaves and flowers of *Ixora* spp. in the park.

Each spider was housed individually in a plastic cylindrical cage (diameter × height: 70 × 85 mm) which was covered with white opaque paper on the sides to prevent visual interaction amongst neighbouring individuals. All spiders were maintained under controlled laboratory conditions of 25 ± 1^{o}C, relative humidity of 70 – 80%, and photoperiod of 12 hr light: 12 hr dark. Additional illumination was provided from full-spectral fluorescent tubes (2% UVB, 10% UVA, 300–700 nm, 36", 30W; Arcadia Natural Sunlight Lamp, Croydon, Angleterre, UK) which simulate natural sunlight, in order to closely mimic the quality of light environment in their natural habitat. Water and 10% sucrose solution were provided *ad libitum* through the use of cotton dental rolls. Spiders were fed twice a week on a mixed diet of fruit flies (*Drosophila melanogaster,* wild type) cultured on traditional banana medium, cricket nymphs (*Acheta domesticus*), and houseflies (*Musca domestica*) (see Lim & Li 2004).

All subadult spiders were inspected daily to check if they had moulted to sexual maturity. If so, the date of final moult was recorded and their age was thus known.

In addition, at 24 hrs following the moult, the spider's body dimensions (length and width of carapace and abdomen) and body mass were measured using an ocular micrometer (resolution 0.01 mm) in a stereomicroscope (Leica MZ16A) and weighing balance (Mettler Toledo AX205, resolution 0.00001g), respectively. For males, spectrophotometric measurements were performed for each individual to record their reflectance spectra on the tenth day after their last moult (for spectral reflectance measurements, see below).

Experimental design and procedures

Mate choice trials were conducted by offering female *C. umbratica* spiders a choice between two randomly selected males, by the use of a choice apparatus (Figure 2-1) which was similar to the one used in earlier studies (Li *et al.* 2008b; Lim *et al.* 2008). The choice apparatus was constructed entirely of quartz glass which permits the transmission of full spectral light (250-700 nm), and facilitates the video-recording of behavioural interactions between the spiders. It consisted of three separate chambers: female viewing chamber (L × W × H: 76 × 25 × 25 mm), and two male display chambers (each chamber: 52 × 25 × 25 mm), so that the males and the female could only interact visually (Figure 2-1). A black opaque cardboard was placed between the male chambers to prevent visual interactions between the males.

The choice apparatus was illuminated by eight full-spectral (300 – 700 nm) fluorescent tubes (48", 110W; Voltarc Ultra Light tubes, U.S.A.) powered by four 120V 50/60Hz electronic ballasts (SUPER-TEK, Naturallighting.com, Houston, TX, USA) and two additional UV-emitting fluorescent tubes (24", 20W;

Blacklite) that were suspended about 1.2 m above the apparatus, providing UV+ white light (250-700 nm) and additional short wavelength illumination. The entire experimental set-up was surrounded by a black opaque curtain with a slit through which video recordings were performed, hence minimizing observer interference as well as providing a standardized black background. A stationary high definition digital video camera (Sony HVR-Z1P HDV 1080i Camcorder) was used to record all behavioural interactions in the experiments.

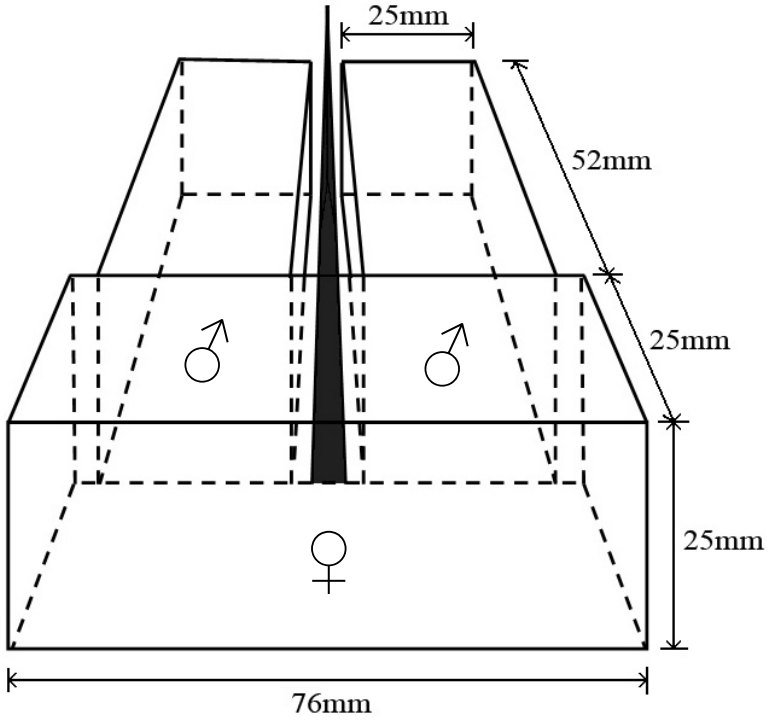

Figure 2-1. Frontal 3-D diagram of the choice apparatus used in mate choice experiments. The symbol ♀ indicates female viewing chamber, and the symbol ♂ indicates male display chamber.

Prior to each mate choice trial, a pair of adult males was randomly selected to participate in the trial, with efforts made to pair individuals of similar mass, size

and age (determined by counting the number of days after the last moult). This was to ensure that morphological differences within each pair of males were minimized. All females used in the trials were similar in body mass, size and age as well. In addition, only virgin males and females were used in the mate choice trials so as to ensure that none of them had any previous encounter with conspecifics which might influence the results of the mate choice experiments. All spiders used were not older than 60 days of age. All trials were conducted between 0800hrs and 1600hrs, during which the spiders are found to be most active in the wild (personal observations).

The standard procedures of each mate choice trial were as such:

1) **Female acclimatization phase 1** – The female spider was introduced into the female viewing chamber and allowed to acclimatize for 5 mins, during which a black opaque paper was placed between the female viewing chamber and the male display chambers.

2) **Control phase 1** – Following the 5-min acclimatization phase, the black opaque paper was removed to present the empty male chambers to the female, upon which the 5-min control phase commenced. The female was video recorded for the entire phase.

3) **Male acclimatization phase** – At the end of the control phase 1, the black opaque cardboard was placed back between the female viewing chamber and the male display chambers. Each male spider was then transferred

into its respective male display chamber, and all individuals were allowed to acclimatize for 5 mins.

4) **Mate assessment phase** – At the end of the acclimatization phase, a 10-min mate assessment phase commenced upon the removal of the black opaque cardboard to allow visual contact between the female and the males. This mate assessment phase was video-recorded throughout the 10 mins.

5) **Female acclimatization phase 2** – At the end of the mate assessment phase, the black opaque paper was placed back between the female viewing chamber and the male display chambers, and the males were removed from their chambers. The female spider was then allowed to acclimatize for 5 mins.

6) **Control phase 2** – Following the 5-min acclimatization phase, the black opaque paper was removed to present the empty male chambers to the female, upon which the 5-min control phase commenced and the female's behaviour video-recorded.

Each female underwent two control phases to ensure that any preference observed was due to the appearance of males during mate assessment rather than a random preference for either of the two chambers. After the end of every trial, each chamber was wiped with 95% alcohol to remove all traces of chemicals that might have been deposited by the spiders, and then left to dry for 30 mins. For

every subsequent trial, a new pair of age and size-matched males was selected, and each of the two individuals randomly assigned to one of the two male display chambers to eliminate the possibility of any side bias. None of the spiders were used more than once in these mate choice trials. Trials were aborted if the female did not observe both of the males, or when any of the males failed to display courtship behaviour to the female after five minutes had elapsed. Trials were also aborted if females showed a preference for any male chamber. A total of 25 successful trials were conducted.

All videos recorded during the control phases were subsequently viewed to determine the duration spent by the female near each male chamber. Recorded videos of the mate assessment phases were also viewed to record these behavioural variables:

1) time spent by the female near each male chamber,
2) duration when the female was directly facing towards each courting male (i.e. watching the male, hereafter female attention),
3) number of times the female was directly oriented towards each courting male, and
4) duration when each male displayed the courtship posture (arched posture with a flexed-up abdomen) to the female (Lim & Li 2004).

These female behavioural variables are deemed to be indicative of the male's success at capturing the female's attention, which are the best estimates of female preference (Li *et al.* 2008b; Lim *et al.* 2008).

Spectrophotometric measurements

To examine differences between the spectral reflectance of *C. umbratica* males, spectrophotometric measurements were performed on the tenth day after their last moult. Measurement procedures were similar to that of Lim & Li (2006b), which were adapted from previously established protocols (Endler 1990; Andersson & Amundsen 1997). Spiders were mildly anaesthetized by carbon dioxide gas for three minutes before measurements were performed. Reflectance in the wavelength range of 250–700 nm was measured with a USB2000 UV/VIS Series fibre-optic spectrometer (Ocean Optics Inc., Dunedin, Florida, U.S.A.). Each reading was taken with a bifurcated fibre-optic probe consisting of a tight bundle of seven 200 mm optic fibres in a stainless steel ferrule (six illuminating fibres around one read fibre). Using a vertical adjustable translation stage (Creative Stars Electro-Optics, Redmond, WA, U.S.A.; resolution 0.01 mm), the probe was positioned perpendicularly at 2 mm above the sample being measured, such that the reading was recorded from a circular spot (diameter 2 mm) on the sample. Illumination was provided by a DH2000 deuterium and tungsten halogen light source (wavelength range 215-2000 nm; Ocean Optics Inc.).

Using the OOIbase32 software (version 2.0.1.4, Ocean Optics Inc.), a WS-1-SL diffuse reflectance white standard (Ocean Optics Inc.) was used to obtain the white reference spectrum while the dark reference was taken with the lights switched off in a dark room, from the matt black background against which each reading was measured. The reflectance spectrum of each specimen was then obtained with respect to these two reference spectra.

For every male, two body parts were measured: dorsal carapace and dorsal abdomen. These were chosen because they are actively displayed during intraspecific interactions. For each body part, five readings were recorded, with each reading obtained from a randomly selected position. The five readings were subsequently averaged to obtain a mean reflectance spectrum which was used for further analyses.

Spectral reflectance characteristics

Three standard colour descriptors are commonly used in the analysis of reflectance spectra (Endler 1990; Hailman 1977). They are hue (wavelength at which the maximal reflectance occurs), chroma (saturation or spectral purity) and brightness (spectral intensity)(Lim & Li 2007). Chroma is estimated as the steepness of the slope (see Figure 2-2a for example), while brightness is estimated as the area under the spectral band (see Figure 2-2b for example).

A typical *C. umbratica* reflectance spectrum (hereafter known as UV-VIS spectrum) consists of two peaks (Figure 2-2a), one in the ultraviolet range (315-400 nm, hereafter known as UV peak), and another in human's visible light range (400-700 nm, hereafter known as VIS peak). An additional weak UVB peak (280-315 nm) exists, but it could only be detected under high integration times at which an additional reflectance spectrum (hereafter known as UVA-UVB spectrum) was obtained in order to analyse the importance of this UVB peak (Figure 2-2b).

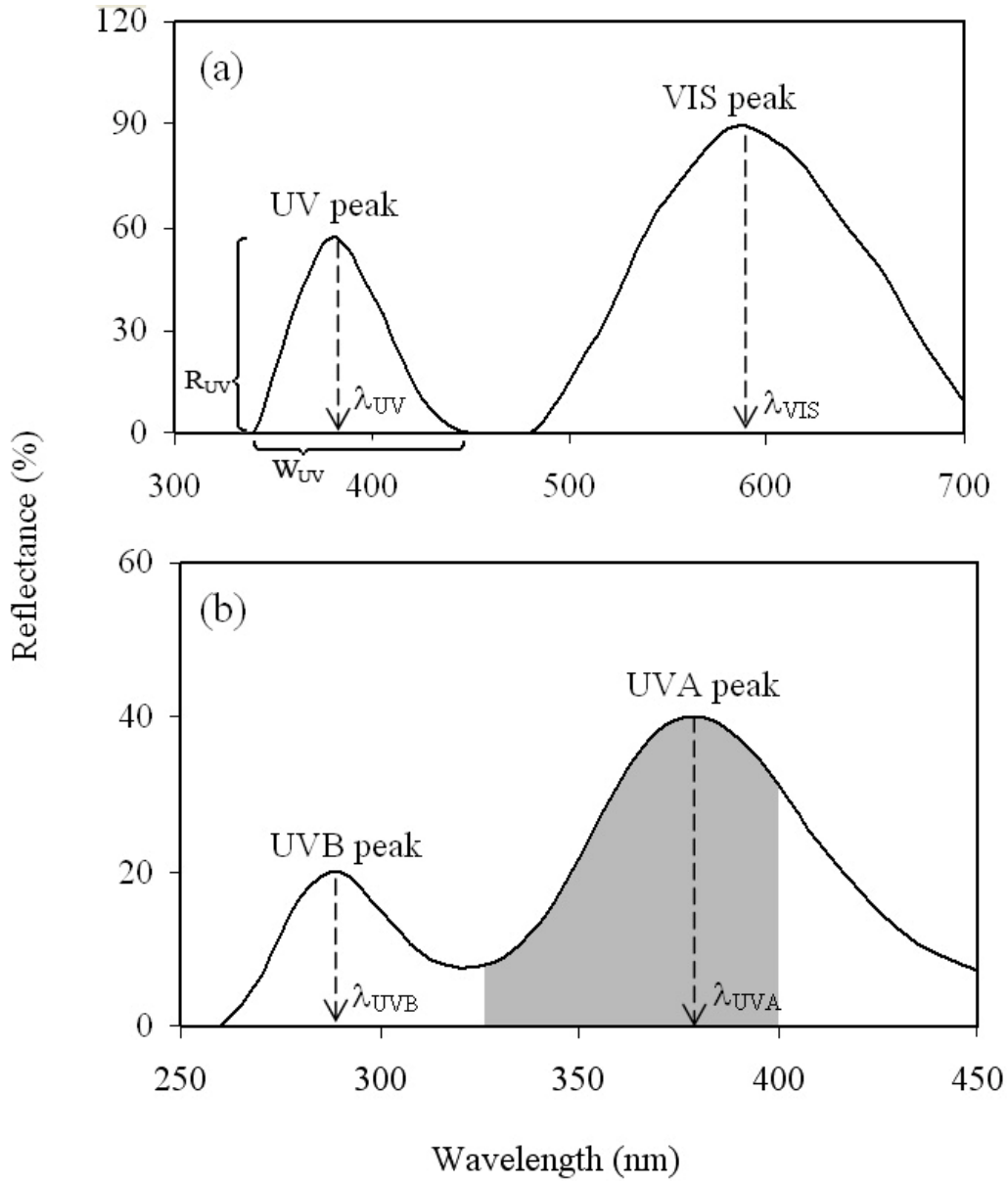

Figure 2-2. Typical reflectance spectra of a male *C. umbratica* carapace. (a) UV-VIS spectrum with UV and VIS peaks. λ_{UV} indicates UV hue, λ_{VIS} indicates VIS hue. (b) UVA-UVB spectrum with UVB and UVA peaks. λ_{UVB} indicates UVB hue, λ_{UVA} indicates UVA hue. Chroma is estimated as the steepness of slope for each waveband (e.g. UV chroma = R_{UV}/W_{UV} , where R_{UV} is the percent reflectance at which λ_{UV} occurs, and W_{UV} is the width of the UV waveband on the x-axis). Brightness is estimated as the area under graph (e.g. UVA brightness is indicated by the shaded region between wavelengths 315 – 400 nm).

Data analysis

All data were tested for normality using the Kolmogorov-Smirnov tests prior to any other statistical analyses. All data were presented as mean ± S.E.. All statistical tests were two-tailed and the significance level was set at $P < 0.05$ ($\alpha = 0.05$), unless otherwise stated. All tests were run using SPSS 16.0 for Windows.

Other than male proximity (amount of time spent by female near male), female attention is also deemed as a reliable indicator of female mate preference (Li *et al.* 2008; Lim *et al.* 2008). Hence in each mate choice trial, the male spider which the female spent more time observing was classified as a preferred male, while the other male spider was classified as non-preferred. Hence, males were classified into two groups: "preferred" and "non-preferred". When female attention on both males was comparable, it was deemed as an inconclusive mate assessment and the data were thus excluded from further analyses. All behavioural data were analysed using paired *t*-tests if they were normally distributed. Otherwise, Wilcoxon signed-rank tests were performed (Zar 1999).

To examine the effects of male mass, size and age on female mate choice, paired *t*-tests were performed for all mass, size and age data to test for differences between the two groups of males (Zar 1999). To examine the effects of male spectral reflectance characteristics on female mate choice, paired *t*-tests were performed for all male spectral reflectance data to test for differences between preferred and non-preferred males (Zar 1999).

RESULTS

Spider mass, size and age

There were no significant differences in body mass, body length, carapace length, carapace width, abdomen length, abdomen width and age between the preferred and non-preferred males (Table 2-1).

Table 2-1. Comparison of mean (± S.E.) mass, size and age between preferred and non-preferred males.

	Preferred	**Non-preferred**	**Paired *t*-test**		
			t	*df*	*p*
Body mass (mg)	0.18 ± 0.01	0.17 ± 0.01	0.436	24	0.672
Body length (mm)	6.77 ± 0.11	6.70 ± 0.11	1.852	24	0.076
Carapace length (mm)	2.67 ± 0.05	2.65 ± 0.04	1.561	24	0.132
Carapace width (mm)	1.69 ± 0.03	1.70 ± 0.03	-0.766	24	0.451
Abdomen length (mm)	4.10 ± 0.07	4.06 ± 0.07	1.102	24	0.281
Abdomen width (mm)	1.72 ± 0.03	1.67 ± 0.02	1.658	24	0.110
Age (days)	29.4 ± 2.9	28.9 ± 2.8	0.255	24	0.801

Mate choice experiments

Comparing the amount of time spent by females near each male chamber, females showed a distinct preference for the preferred group over the non-preferred group in the mate assessment phase ($Z = -2.472$, $N = 25$, $p = 0.014$), but no preference for either group in the two control phases (Control 1: $Z = -0.672$, $N = 25$, $p = 0.502$; Control 2: $Z = -0.579$, $N = 25$, $p = 0.563$; Figure 2-3a). Females spent significantly more time watching males in the preferred group compared to those in the non-preferred group ($Z = -4.373$, $N = 25$, $p < 0.001$; Figure 2-3b). Additionally, females directed their gaze towards preferred males more frequently than non-preferred males ($Z = -3.609$, $N = 25$, $p < 0.001$; Figure 2-3c). There were no significant differences in the duration of male courtship displays between the preferred and non-preferred groups ($t_{24} = -0.447$, $p = 0.659$; Figure 2-3d).

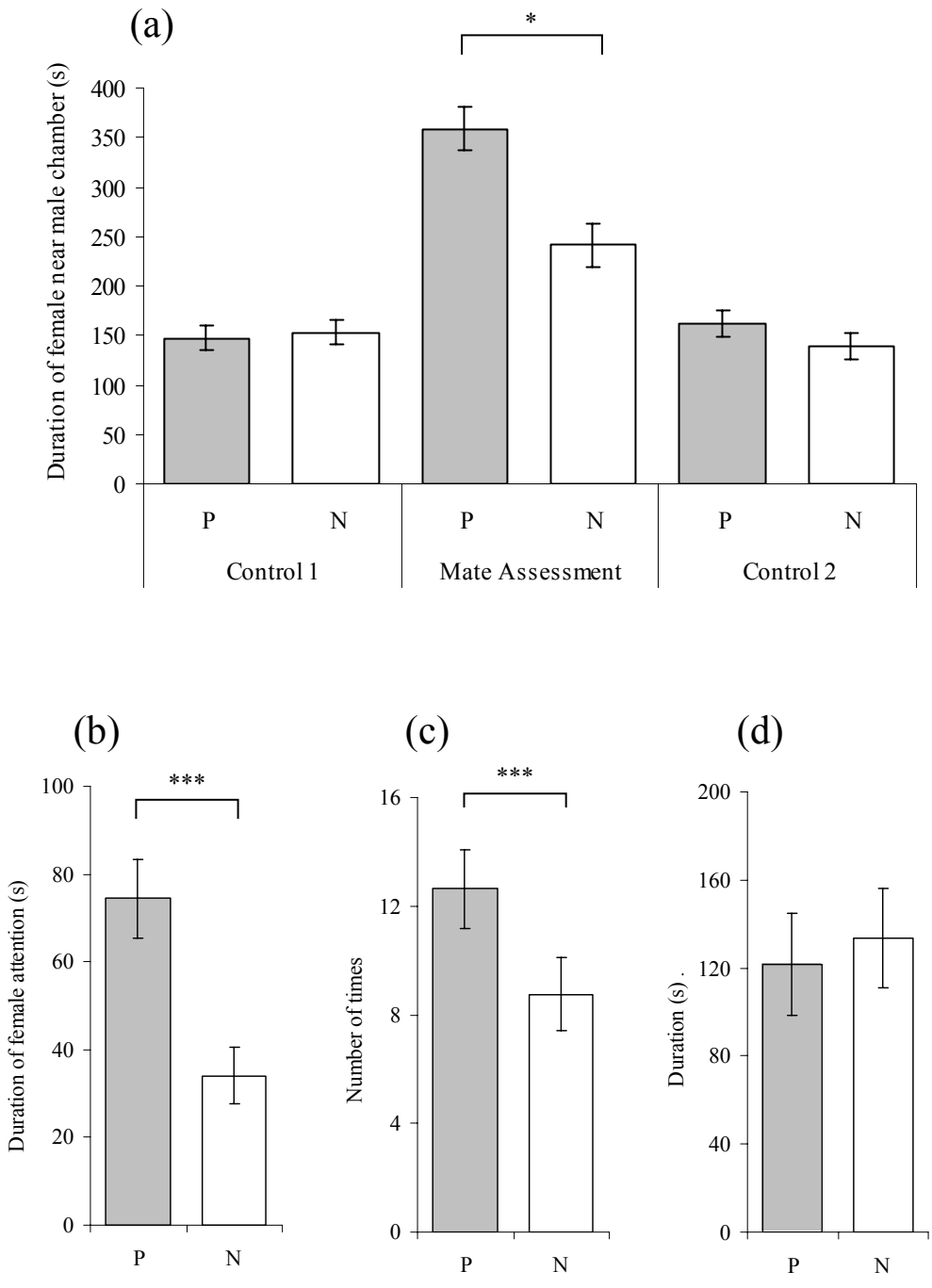

Figure 2-3. (a) Mean (± S.E.) time (s) spent by the female near the male chamber. (b) Mean (± S.E.) time (s) spent by the female watching the male. (c) Mean (± S.E.) number of times the female was oriented towards the courting male. (d) Mean (± S.E.) time (s) spent by the male displaying courtship behaviour. P denotes preferred males, N denotes non-preferred males. * indicates $p < 0.05$, *** indicates $p < 0.001$.

Spectral reflectance characteristics

There were two discrete peaks in the UV-VIS reflectance spectra of preferred and non-preferred males (Figure 2-4), while the UVA-UVB reflectance spectra lacked a distinctive trough between the two bands (Figure 2-5). Hence, chroma for UVA and UVB bands could not be accurately estimated (Lim & Li 2006b).

UV-VIS spectral characteristics

For both dorsal carapace and abdomen, there were no significant differences in UV hue and VIS hue between preferred and non-preferred males. However, preferred males had higher chroma and brightness in both UV and VIS wavelengths when compared to non-preferred males (Table 2-2; Figure 2-4).

UVA-UVB spectral characteristics

For both dorsal carapace and abdomen, preferred and non-preferred males had similar UVA hue and UVB hue, but preferred males were significantly UVA and UVB brighter than non-preferred males (Table 2-3; Figure 2-5).

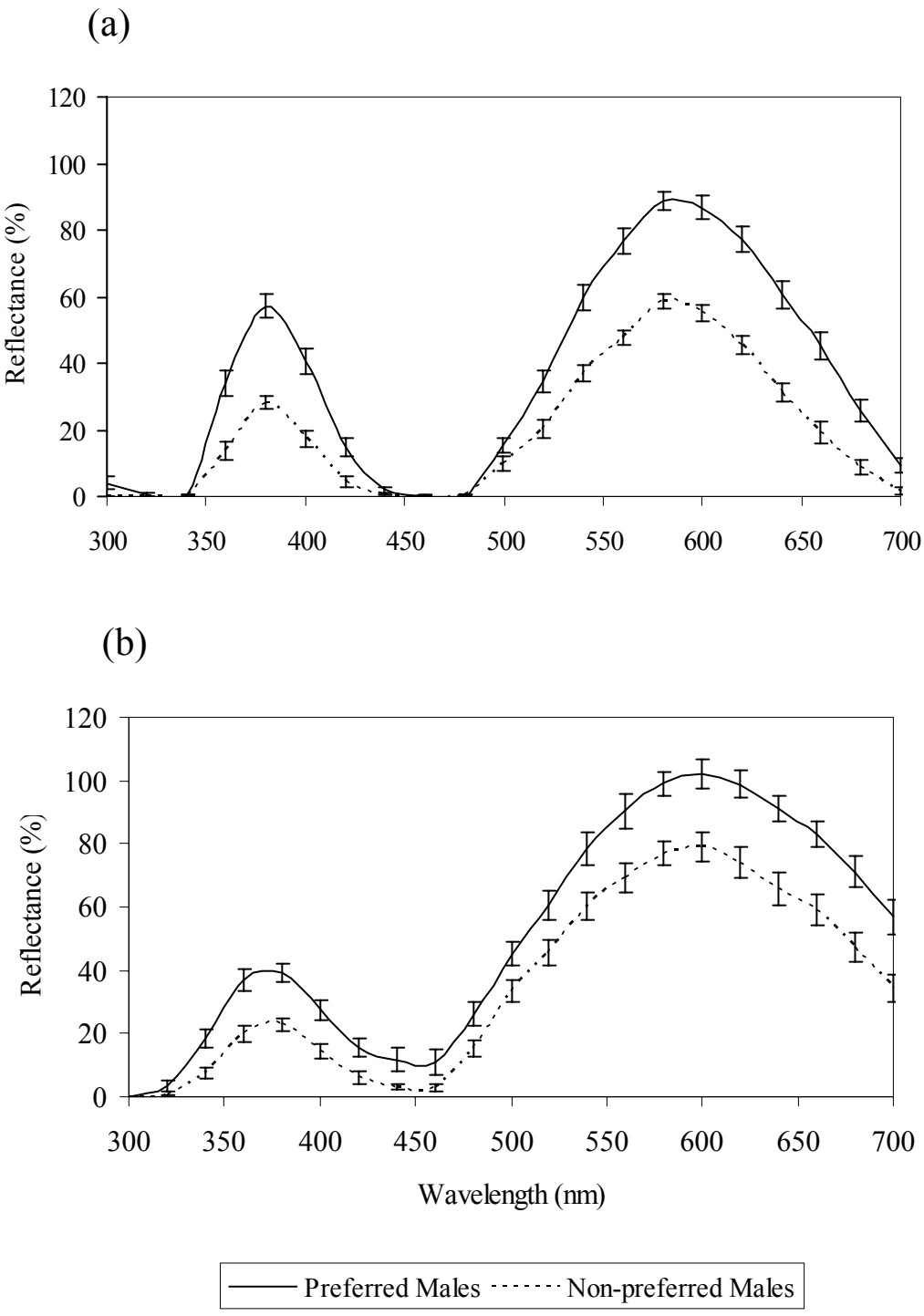

Figure 2-4. (a) UV-VIS reflectance spectrum of the dorsal carapace of preferred and non-preferred males. (b) UV-VIS reflectance spectrum of the dorsal abdomen of preferred and non-preferred males. Each point shows the mean (± S.E.) of 25 male spiders.

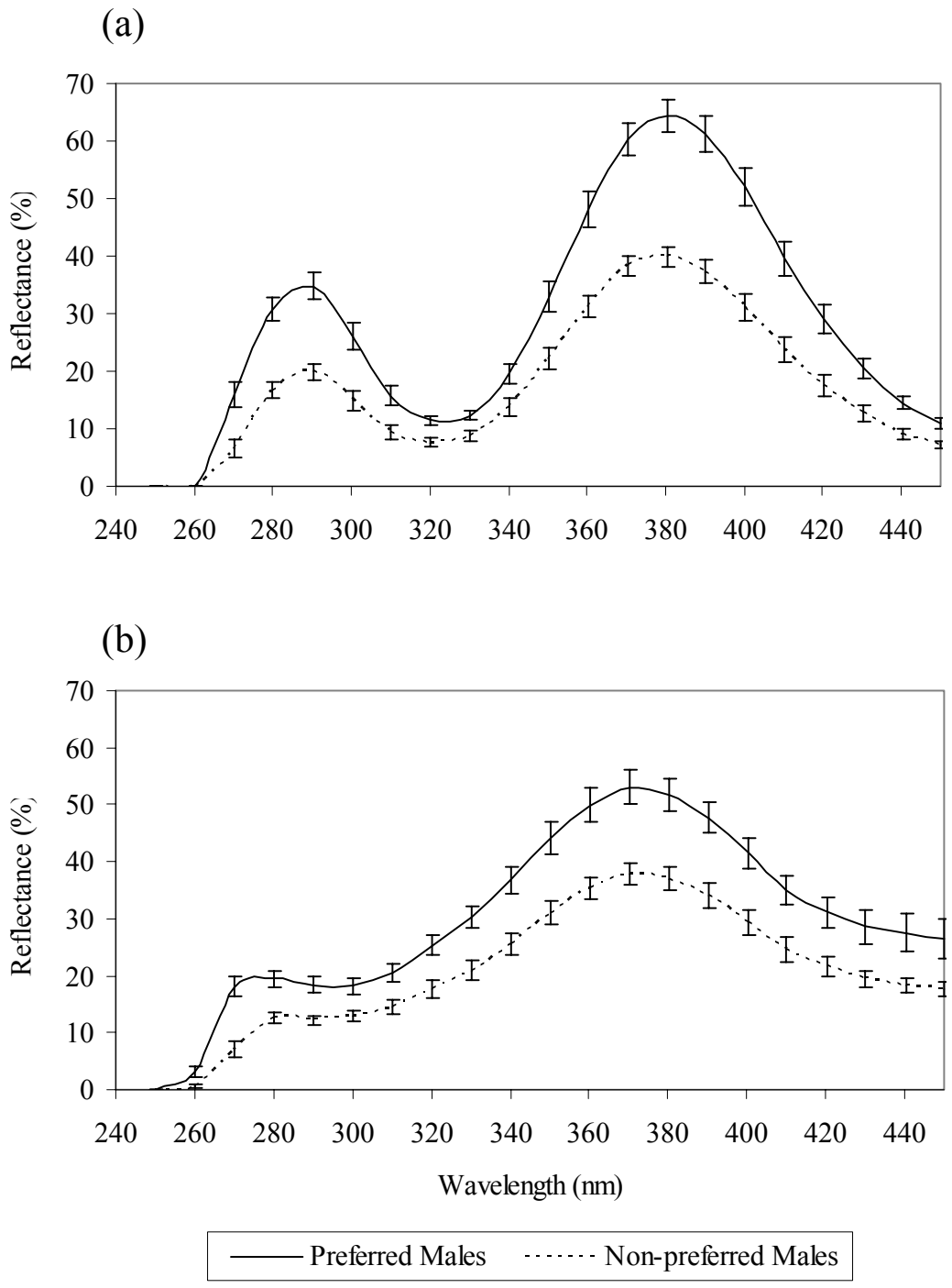

Figure 2-5. (a) UVA-UVB reflectance spectrum of the dorsal carapace of preferred and non-preferred males. (b) UVA-UVB reflectance spectrum of the dorsal abdomen of preferred and non-preferred males. Each point shows the mean (± S.E.) of 25 male spiders.

Table 2-2. Comparison of UV-VIS spectral characteristics between preferred and non-preferred males.

Body part	Spectral traits	Preferred	Non-preferred	Paired *t*-test		
				t	*df*	*p*
Carapace	UV Hue (nm)	379.9 ± 1.8	378.4 ± 2.1	0.530	24	0.601
	UV Chroma (%nm^{-1})	0.64 ± 0.03	0.41 ± 0.02	8.212	24	<0.001*
	UV Brightness (%nm)	2306.7 ± 162.0	1025.3 ± 78.4	7.684	24	<0.001*
	VIS Hue (nm)	593.2 ± 2.3	590.4 ± 2.4	0.953	24	0.350
	VIS Chroma (%nm^{-1})	0.41 ± 0.01	0.30 ± 0.01	8.228	24	<0.001*
	VIS Brightness (%nm)	12267.2 ± 594.3	7139.2 ± 386.7	8.769	24	<0.001*
Abdomen	UV Hue (nm)	373.1 ± 4.2	372.0 ± 2.4	0.227	24	0.822
	UV Chroma (%nm^{-1})	0.46 ± 0.02	0.30 ± 0.02	6.369	24	<0.001*
	UV Brightness (%nm)	2274.4 ± 173.5	1186.2 ± 123.1	7.766	24	<0.001*
	VIS Hue (nm)	598.6 ± 6.7	598.0 ± 2.9	0.083	24	0.934
	VIS Chroma (%nm^{-1})	0.38 ± 0.01	0.30 ± 0.01	5.833	24	<0.001*
	VIS Brightness (%nm)	18543.4 ± 718.3	13348.1 ± 895.7	6.187	24	<0.001*

Table 2-3. Comparison of UVA-UVB spectral characteristics between preferred and non-preferred males.

Body part	Spectral traits	Preferred	Non-preferred	Paired *t*-test		
				t	*df*	*p*
Carapace	UVB Hue (nm)	287.2 ± 1.3	285.9 ± 1.5	0.648	24	0.523
	UVB Brightness (%nm)	947.3 ± 65.6	545.9 ± 46.0	6.701	24	<0.001*
	UVA Hue (nm)	380.4 ± 1.8	378.3 ± 2.1	0.789	24	0.438
	UVA Brightness (%nm)	3403.2 ± 142.7	2173.0 ± 88.7	7.737	24	<0.001*
Abdomen	UVB Hue (nm)	277.4 ± 2.1	279.9 ± 1.9	-0.976	23	0.339
	UVB Brightness (%nm)	684.1 ± 43.5	472.9 ± 26.6	4.898	24	<0.001*
	UVA Hue (nm)	373.0 ± 2.6	372.2 ± 2.5	0.240	24	0.812
	UVA Brightness (%nm)	3635.4 ± 172.2	2612.1 ± 121.6	8.362	24	<0.001*

DISCUSSION

In this study, a series of mate choice experiments were performed to identify the UV-reflective characteristics that may be important in female mate choice in *C. umbratica*. My results show that females exhibited a distinct preference for males with higher chroma and brightness in both UV and visible (VIS) wavelengths. Preferred males were also found to have brighter carapaces and abdomens in the UVB and UVA wavelengths when compared to non-preferred males. These suggest that UV brightness of males is important in female mate choice in this salticid species.

A male's morphological traits are known to play an important role in female mate choice decisions (Karino & Urano 2008; Karino *et al.* 2010; Siitari *et al.* 2002b). Since preferred and non-preferred males were similar in mass and size in this study, male mass and size are thus unlikely to account for the observed female preference. Preference for either of the two male chambers is also ruled out as females exhibited no preference for either of them during the two control phases. This again indicates that the female's preference is due to the presence of courting males.

Previous studies have shown that male courtship behaviour has a significant effect on female mate choice (Kodric-Brown 1993; Kodric-Brown & Nicoletto 1996; Slagsvold & Viljugrein 1999). However, my findings show that there was no significant difference in courtship duration between the two groups of males. Hence, male courtship intensity is ruled out in this study. Nevertheless, preferred

males attracted significantly more female attention than non-preferred males, thus suggesting that the female's preference was due to some other factor rather than the intensity of males courtship displays.

Many studies of female mate preference have demonstrated that UV and VIS reflectance traits are important factors of a male's mating success (Bennett *et al.* 1996, 1997; Kodric-Brown & Johnson 2002; Li *et al.* 2008b; Lim & Li 2008; Pearn *et al.* 2001; Rick *et al.* 2006; Smith *et al.* 2002). Similarly, the results of this study demonstrated that UV and VIS reflectance traits are important to *C. umbratica* females for making mate choice decisions. Females showed a distinct preference for males with higher UV and VIS brightness and chroma.

Interestingly, when examining the UVA-UVB spectra, females exhibited a clear preference for males with brighter UVA and UVB reflectance. Although some animals are known to reflect and respond to UVB (e.g. Han *et al*. 2007; Li *et al.* 2008a, 2008b; Mazza *et al*. 1999, 2002; McGraw 2004), animals were generally assumed to be unable to distinguish UVB from other wavelengths. Therefore very few studies have been conducted to examine the adaptive significance of UVB reflectance in animal communication (Smith & Macagno 1990; Tovée 1995). Li *et al.* (2008a, 2008b) were the first to provide evidence that the jumping spider *Phintella vittata* uses UVB in intra-specific communication. They have also demonstrated that females use UVB reflectance as signals in mate choice decisions in *P. vittata*. The reflectance spectra of *C. umbratica* has an UVB band and an UVA band (Lim & Li 2006b), but the relative importance of these two bands is currently unknown. Although it is likely that the weak UVB band has a

minimal role compared to the UVA band, future studies should be conducted to investigate the relative importance of UVA and UVB in female mate choice and animal communication.

My results clearly indicate that *C. umbratica* females are capable of distinguishing between males that differ in their spectral reflectance traits. Female preference is positively related to the brightness and chroma of a male's carapace and abdomen for both UV and VIS wavebands. However, the relative importance of these two spectral reflectance traits (brightness and chroma) remains unknown. Hence it is essential that further studies are conducted to examine this.

Numerous studies have illustrated that UV reflectance is relatively more important than VIS reflectance in female mate choice (Hunt *et al.* 1999; Li *et al.* 2008b; Lim & Li 2008). However, based on the results of this study, such a conclusion could not be made. Therefore, further studies with more appropriate experimental designs would be required in order to demonstrate this.

Many studies have provided evidence that male UV-reflecting ornaments function in the context of sexual selection, in particular female mate choice (Garcia & Perera 2002; Hunt *et al.* 1999; Johnsen *et al.* 1998; Kodric-Brown and Johnson 2002; Rick *et al.* 2006; Smith *et al.* 2002; White *et al.* 2003). Such UV-reflecting ornaments are determinants of a male's mating success, and may serve the function of conveying crucial information such as male quality to the female which is important for making mate choice decisions. UV-reflecting

ornaments may be indicative of the male's qualities such as state of health, nourishment, vigour and genes (Darwin 1871; Jones & Ratterman 2009). In addition, they may also be indicators of the male's territorial quality (Siebeck 2004, Siefferman & Hill 2005), social dominance (Woodcock *et al.* 2005), and parental investment (Johnsen *et al.* 2005; Limbourg *et al.* 2004; Siefferman & Hill 2005).

Research has shown that many sexual-selected ornaments depend on the condition of the individual that bears it (Delhey *et al.* 2006; Doucet 2002; Keyser & Hill 1999, 2000; Mougeot *et al.* 2005). For example, previous studies have shown that male condition-dependent ornaments are reliable indicators of parasite load (Mougeot *et al.* 2005), sexual maturity (Jouventin *et al.* 2005), immunocompetence, and sperm quality (Peters *et al.* 2004). A study conducted by Lim and Li (2007) revealed that UV reflectance in *C. umbratica* is indicative of a male's age and hunger level. The UV peaks of older males occur at shorter wavelengths compared to younger males, while the carapaces of younger males are brighter for VIS wavelengths. Moreover, well-fed males have brighter abdomens in both the UV and VIS ranges when compared to starved males, thus demonstrating that UV reflectance in *C. umbratica* is indeed a condition-dependent trait. However, more studies should be conducted to elucidate other factors that UV reflectance might be dependent on (see Chapter 4).

If females mate with males that honestly advertise their high quality via displays of their condition-dependent UV-reflecting ornaments, females should gain

fitness benefits as a consequence of their mate choice (Darwin 1871; Johnstone 1995, 1997; Cuthill *et al.* 2000; Zahavi & Zahavi 1997). Such benefits may be direct (female fitness) or indirect (genetic effects on offspring). However, the maintenance of female mate choice in *C. umbratica* is currently poorly understood. Hence, further studies should focus on investigating the fitness consequences of female mate choice in *C. umbratica* (see Chapter 3), in hope of shedding some light on the evolution of UV-reflecting male ornaments and female mate choice in this jumping spider particularly and other animals in general.

CONCLUSION

A study by Lim *et al.* (2008) revealed that *C. umbratica* males with UV-reflecting ornaments captured significantly more female attention when compared to males without, thus illustrating that the presence of UV reflectance is important to a male's mating success. However, the importance of each UV spectral characteristic remained unidentified. My study is the first to illustrate that UV brightness and chroma are important criteria which are used by *C. umbratica* females when making mate choice decisions. Female preference was positively correlated to UV brightness and chroma, possibly attributable to the information which they might convey to females. The fitness consequences of UV-based mate choice, as well as the likelihood that UV-reflecting ornaments are reliable indicators of male quality, were subsequently examined in the following chapters of this thesis (Chapters 3 and 4).

CHAPTER 3

Fitness Consequences of UV-Based Female Mate Choice in the Jumping Spider *Cosmophasis umbratica*

Abstract. Females of many animals prefer males with more colourful and brighter UV ornamentation. Yet little is known about the ultimate causes of UV-based female mate choice. In this study, I evaluated the effects of UV-based female mate choice on female and offspring fitness in a jumping spider *Cosmophasis umbratica*. Preferred and non-preferred males were mated with randomly selected females, and the reproduction of females and development of their offspring were monitored. Females that mated with preferred males produced similar number of offspring as those that mated with non-preferred males, hence supporting the view that females do not receive direct benefits in terms of fertility as a result of their mate choice. Nonetheless, hatchlings fathered by preferred males were larger at emergence from the nest when compared to those fathered by non-preferred males. Juvenile spiders fathered by preferred males also survived longer, grew faster and were larger than those fathered by non-preferred males. Females mated with preferred males that were UV brighter also produced sons that were UV brighter. This study is the first to demonstrate that preferred males confer higher performance on their offspring, allowing *C. umbratica* females to enjoy indirect genetic benefits as a result of their choice.

Keywords: Jumping spider, *Cosmophasis umbratica*, ultraviolet light, sexual selection, indirect benefits, good genes.

INTRODUCTION

Many studies have shown that male UV-reflecting ornaments function in the context of sexual selection (Alonso-Alvarez *et al.* 2004; Cuthill *et al.* 2000; Siefferman & Hill 2005). Particularly, much evidence supports the view that such ornaments play an important role in female mate choice (Garcia & Perera 2002; Hunt *et al.* 1999; Johnsen *et al.* 1998; Kodric-Brown & Johnson 2002; Li *et al*. 2008b; Lim *et al*. 2008; Rick *et al.* 2006; Smith *et al.* 2002; White *et al.* 2003). Nevertheless, there is still much debate over the ultimate causes of such a female mate choice.

Several models have been proposed to explain the evolution of female mate choice. The direct benefits model suggests that females choose males because they provide immediate benefits such as nuptial gifts (Gwynne 1984), parental care (Ostlund & Ahnesjo 1998; Preault *et al.* 2005), protection (Borgia 1981; Galimberti *et al.* 2000), parasite avoidance (Worden & Parker 2005), or increased fertility (Markow *et al.* 1978; Nakatsuru & Kramer 1982). The good genes model suggests that the male's trait is a condition-dependent indicator of good genetic quality (Zahavi 1975), and thus the female gains indirect benefits in the form of increased offspring viability (Lopuch & Radwan 2009; Mead & Arnold 2004; Moore 1994; Pomiankowski 1988; Punzalan *et al.* 2008). Under the Fisherian sexy son model, the ornament gene is selected for together with the preference gene (Jones *et al.*1998; Kirkpatrick 1982; Lande 1981), therefore females benefit because they will produce attractive sons (Weatherhead & Robertson 1979). The sensory exploitation model predicts that females may not gain any benefits at all

because male ornaments merely evolved to take advantage of pre-existing sensory-bias in females (Fleishman 1992; Ryan 1998; Smith *et al.* 2004). Finally, there are also the models of genetic compatibility and sexual conflict (Arnqvist & Rowe 2005; Maan & Taborsky 2008; Demary & Lewis 2007; Ryan & Altmann 2001).

Several studies have revealed that UV-based male ornaments are correlated with male quality in a range of animals (Delhey *et al.* 2006; Doucet 2002; Doucet *et al.* 2005, 2006; Kemp 2006; Keyser & Hill 1999, 2000; Mougeot *et al.* 2005; Peters *et al.* 2006). For instance, a study had determined that UV reflectance in *C. umbratica* is condition-dependent, and is indicative of male age and hunger level (Lim & Li 2007). UV-reflecting ornaments are possible determinants of a male's mating success, and may serve the function of conveying crucial information such as male quality to the female which is important for making mate choice decisions. In fact, UV-reflecting ornaments may be indicative of male qualities such as state of health (Pike *et al.* 2007), nourishment, vigour and good genes (Darwin 1871; Jones & Ratterman 2009). In addition, they may also be indicators of the male's territorial quality (Siebeck 2004, Siefferman & Hill 2005), social dominance (Woodcock *et al.* 2005), and parental investment (Johnsen *et al.* 2005; Limbourg *et al.* 2004; Siefferman & Hill 2005). Hence, by assessing males based on their ornaments, females may be able to make adaptive mate-choice decisions.

According to intersexual selection theory, if females mate with males that advertise their high quality via displays of their condition-dependent UV-reflecting ornaments, females should gain fitness benefits as a consequence of their mate choice (Cuthill *et al.* 2000; Darwin 1871; Johnstone 1995, 1997;

Zahavi & Zahavi 1997). Such benefits may be direct (female fitness) or indirect (genetic effects on offspring), and must be present if the evolution of female mate choice for UV-reflecting male ornaments is due to their reliable indication of male quality. In *C. umbratica*, males have not been observed to provide any form of direct benefits such as nuptial gifts and parental care. Moreover, no studies have been conducted to examine the benefits that males have to offer to females. In fact, the fitness consequences of UV-based female mate choice in many animals, including *C. umbratica*, are currently unknown. Hence, the objective of this part of my research is to evaluate the fitness consequences of *C. umbratica* female mate choice. I first assessed whether females could gain direct benefits for choosing males by examining the differences in the number of offspring produced by females mated with either preferred or non-preferred males. However, females may gain indirect genetic benefits if offspring sired by preferred males have higher fitness than offspring sired by non-preferred males. Thus, I examined whether females given a choice of mates produced offspring with higher viability, growth rate, large size, and being attractive relative to females mated with non-preferred males.

MATERIALS AND METHODS

Experimental design and procedures

Female adult spiders were randomly assigned to two groups (attractive and unattractive), and their mass, length and age were controlled for. For the attractive group, each female was allowed to mate with one male spider in the preferred group from the mate choice experiments in Chapter 2 (see Figure 2-3). As for the unattractive group, each female was allowed to mate a non-preferred male. For both groups, the mating process was conducted in a Petri dish (diameter 90 mm) covered by a clear glass panel which allowed the transmission of full spectral light (250-700 nm). The mating arena was illuminated by eight full-spectral fluorescent tubes (48", 110W; Voltarc Ultra Light tubes, U.S.A.) that were suspended 1.2 m above, providing full spectral white light (250-700 nm) illumination which mimics natural sunlight. To minimize observer interference, the mating arena was surrounded by a black opaque curtain with a slit through which video recordings could be performed using a stationary high definition digital video camera (Sony HVR-Z1P HDV 1080i Camcorder). The spiders were allowed to interact and mate for 1 hr, and the process was video recorded and subsequently viewed to determine if they had mated or not (defined as the male inserting its palps into the female's epigyne). All matings were conducted between 0800 and 1600 hrs, during which the spiders were obeserved to be most active in the wild (personal observations). A total of 34 successful matings (attractive group: 13, unattractive group: 21) were conducted.

Cosmophasis umbratica spiders build nests that resemble a flattened tube which is made of silk and has entrances at each of its two ends (Lim & Li 2004). Before oviposition (i.e. the laying of eggs), the female seals the entrances with silk and encloses itself inside the nest where it will lay a clutch of spherical, yellowish-white eggs. Subsequently, the female will remain inside the nest with the eggs until they have hatched (approximately 13 days after oviposition, personal observations) and the postembryos have moulted once within the nest (approximately 20 days after hatching, personal observations). At approximately 35 days after oviposition, the female cuts open the nest's entrance and leaves, allowing the "first instar" spiderlings (for definition, see Hallas 1988) to emerge and disperse.

Females that had mated successfully were monitored daily to check for the presence of eggs so as to record the date of oviposition. The nests were monitored daily to check for the hatching of eggs and the emergence of spiderlings from the nest. However, it was not feasible to account for the hatching date of each egg and the date of the first moult for each postembryo within the silken nest. Therefore, these data were not collected, and only the date of oviposition and spiderling emergence were recorded. Data from a total of 20 females were collected (attractive group, n = 10; unattractive group, n = 10).

To evaluate the differences in offspring fitness between the two groups of females, the following data were collected:

1) Fertility (defined as the number of hatchlings produced by each female, as opposed to fecundity which is the total number of eggs produced);
2) Embryo development time (defined as the time interval in days between oviposition and spiderling emergence);
3) Hatchling size;
4) Juvenile survivorship;
5) Juvenile development time;
6) Juvenile size; and
7) Male offspring spectral reflectance.

Survivorship, development time and size of juveniles were monitored until they reached sexual maturity or died (Li & Jackson 1997). Spider mortality and moulting were checked and recorded daily, and the exuviae were collected. Body lengths and five carapace dimensions (Figure 3-1; Li & Jackson 1997) of exuviae were measured 24 hours after each moult using an ocular micrometer (resolution 0.01 mm) in a stereomicroscope (Leica MZ16A). Spiders that moulted to adulthood were also measured at 24 hours after moulting. The reflectance data of all male offspring were measured on the tenth day after its moult using the same protocol as in Chapter 2 (also see below), and their reflectance spectra were explored using the software AVICOL (Gomez 2006). Subsequently, spectral reflectance characteristics (i.e. hue, chroma and brightness) were calculated manually (see Chapter 2 for details).

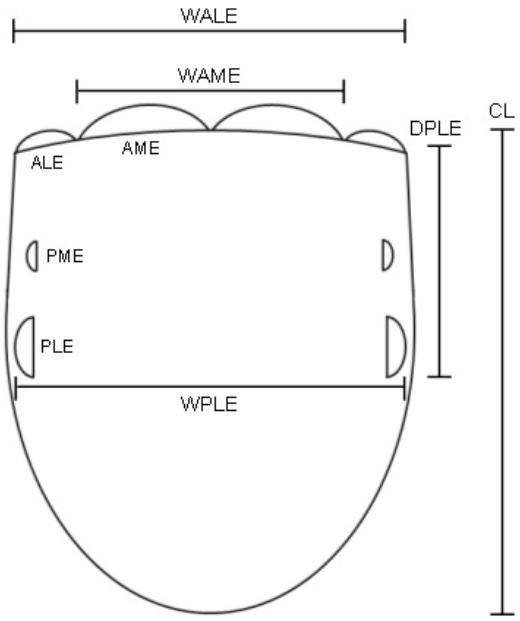

Figure 3-1. Diagram of a *Cosmophasis umbratica* carapace (dorsal view). ALE: anterior lateral eyes; AME: anterior median eyes; PLE: posterior lateral eyes. The bars indicate the five carapace dimensions that were measured: CL, carapace length; DPLE, distance between ALE and PLE; WAME, WALE, and WPLE, distance between the outside margins of AME, ALE, and PLE respectively.

Spider maintenance

All hatchlings were separated and individually housed within 7 days upon emergence. Each spider was housed individually in a plastic cylindrical cage (diameter × height: 70 × 85 mm) and maintained under controlled laboratory conditions of 25 ± 1^{o}C, relative humidity of 70 – 80%, and photoperiod of 12hr light:12hr dark. Additional illumination was provided from full-spectral fluorescent tubes (2% UVB, 10% UVA, 300–700 nm, 36", 30W; Arcadia Natural Sunlight Lamp, Croydon, Angleterre, UK) which simulate natural sunlight, in order to closely mimic the illumination in their natural habitat.

Water and 10% sucrose solution were provided *ad libitum* through the use of dental rolls. Pilot experiments revealed that some hatchlings starved to death because they experienced difficulties capturing wild type fruit flies (*Drosophila melanogaster*). In order to prevent this, vestigial (wingless) fruit flies were given to newly emerged spiderlings during the first 14 days to ensure that they could capture their first meal. Spiders that starved to death because they failed to feed were excluded from the experiment. After then, spiders were fed on a mixed diet of houseflies (*Musca domestica*), small cricket nymphs (*Acheta domesticus*), wild type fruit flies (*Drosophila melanogaster*) cultured on traditional banana medium, and wild type fruit flies cultured on instant *Drosophila* medium (Formula 4-24, Plain. Carolina Biological Supply Company) added with amino acids (22090 Casein Hydrolysate, Sigma-Aldrich). Previous studies have shown that fruit flies cultured on banana medium lacked certain nutrients required by spiders, but laboratory-raised spiders enjoyed improved survivorship and growth rates when fed with fruit flies cultured on Carolina medium added with amino

acids (Mayntz & Toft 2001). All spiders were fed three times a week, with prey provided in excess to ensure that the spiders never starved.

Spectrophotometric measurements

To examine differences in male offspring spectral reflectance between the attractive group and unattractive groups, spectrophotometric measurements were performed on the tenth day after the last moult of each male offspring. Measurement procedures were the same as in the previous chapter (for details, see Chapter 2), which were similar to that of Lim & Li (2006b). Spiders were mildly anaesthetized by carbon dioxide gas for three minutes before measurements were performed. Reflectance in the wavelength range of 250–700 nm was measured from two body parts of every spider: dorsal part of the carapace and abdomen. For each body part, five readings were recorded, with each reading obtained from a randomly selected position. The five readings were subsequently averaged to obtain a reflectance spectrum which was used to obtain the hue, chroma and brightness of the UV and VIS wavebands.

Data analysis

All data were tested for normality using the Kolmogorov-Smirnov tests prior to any other statistical analyses. All data were presented as mean ± S.E. All statistical tests were two-tailed and the significance level was set at $P < 0.05$ ($\alpha = 0.05$), unless otherwise stated. All tests were run using SPSS 16.0 for Windows.

To check that effects of spider mass, size and age were controlled for, two-sample *t*-tests were performed for all normally-distributed mass, size and age data to test for parental differences between the attractive and unattractive groups.

For each individual mother spider, data from all of its respective offspring were averaged to derive offspring data such as embryo development time, hatchling size, survivorship, juvenile development time, size, and spectral reflectance characteristics, so as to control for the effect of genetic similarities among offspring which shared the same parents.

Two-sample *t*-tests were run to test for differences in fertility and embryo development time between the attractive and unattractive groups. Mann-Whitney *U* tests were used to test the differences in hatchling size, offspring survivorship, development time and size between the attractive and unattractive groups because of the small sample size which decreased with each following instar due to high mortality. Developmental time and size data for adult males were excluded from statistical analyses because of their small sample sizes which were resulted by low survivorship of adult male offspring, particularly in the unattractive group. Mann-Whitney *U* tests were also performed to examine the effects of female mate choice on male offspring spectral reflectance by comparing the spectral differences of sons produced by females from attractive and unattractive groups. Data from subadult males was used for comparisons because of the extremely small sample sizes of males that survived till adulthood, particularly in the unattractive group.

RESULTS

Parental mass, size and age

There were no significant differences in maternal (Table 3-1) and paternal (Table 3-2) body mass, body length, carapace length, carapace width, abdomen length, abdomen width and age between the attractive and unattractive groups.

Table 3-1. Comparison of maternal mass, size and age between the females of attractive and unattractive groups.

	Attractive (*N*=10)	**Unattractive (*N*=10)**	**Two-sample *t*-test**		
			t	***df***	***p***
Body mass (mg)	0.170 ± 0.004	0.168 ± 0.007	0.342	18	0.736
Body length (mm)	6.55 ± 0.09	6.54 ± 0.12	0.052	18	0.959
Carapace length (mm)	2.35 ± 0.03	2.36 ± 0.03	-0.217	18	0.830
Carapace width (mm)	1.56 ± 0.02	1.56 ± 0.02	0.311	18	0.760
Abdomen length (mm)	4.20 ± 0.08	4.19 ± 0.12	0.122	18	0.904
Abdomen width (mm)	2.57 ± 0.03	2.59 ± 0.06	-0.311	18	0.760
Age (days)	55.5 ± 9.5	51.3 ± 12.1	0.206	18	0.839

Table 3-2. Comparison of paternal mass, size and age between the males of attractive and unattractive groups.

	Attractive (*N*=10)	**Unattractive (*N*=10)**	**Two-sample *t*-test**		
			t	***df***	***p***
Body mass (mg)	0.185 ± 0.005	0.181 ± 0.006	0.605	18	0.552
Body length (mm)	6.89 ± 0.17	6.66 ± 0.19	0.905	18	0.378
Carapace length (mm)	2.74 ± 0.06	2.62 ± 0.06	1.446	18	0.165
Carapace width (mm)	1.74 ± 0.04	1.69 ± 0.04	0.892	18	0.384
Abdomen length (mm)	4.15 ± 0.12	4.04 ± 0.14	0.622	18	0.542
Abdomen width (mm)	1.73 ± 0.04	1.63 ± 0.05	1.620	18	0.123
Age (days)	65.0 ± 12.9	50.3 ± 16.8	0.695	18	0.496

Mating experiments

Thirteen females that mated with non-preferred males were observed to consume their eggs before they hatched, while three females that mated with preferred males were observed to do so ($\chi^2 = 4.859$, $df = 1$, $p = 0.028$). Offspring data were collected from a total of ten females from the attractive group and ten females from the unattractive group which produced eggs that hatched successfully.

Female fertility

There was no significant difference in the number of offspring produced by females between the attractive and unattractive groups (t_{18} = 1.09, p = 0.29; Figure 3-2).

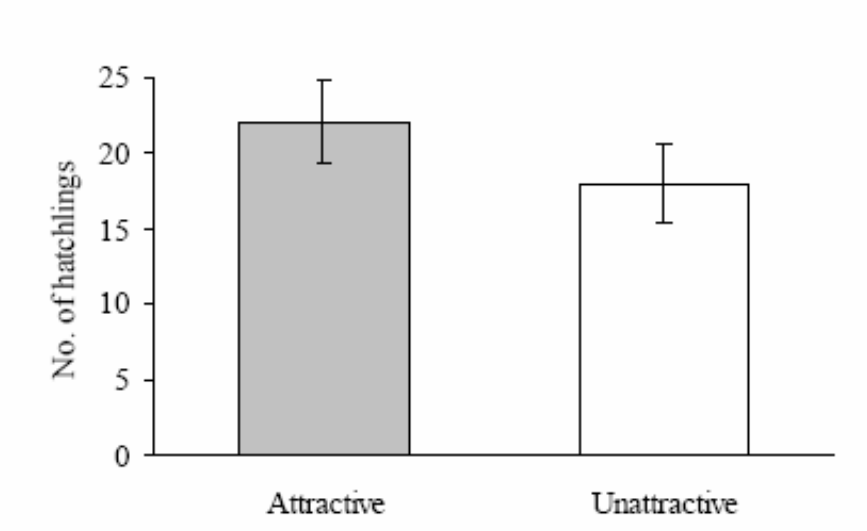

Figure 3-2. Fertility (mean ± S.E. number of hatchlings produced) of females in the attractive and unattractive groups.

Embryo development time

Offspring produced by females of the attractive group hatched slightly earlier than those produced by females of the unattractive group (Figure 3-3), but this difference was not significant (t_{18} = -0.697, p = 0.495).

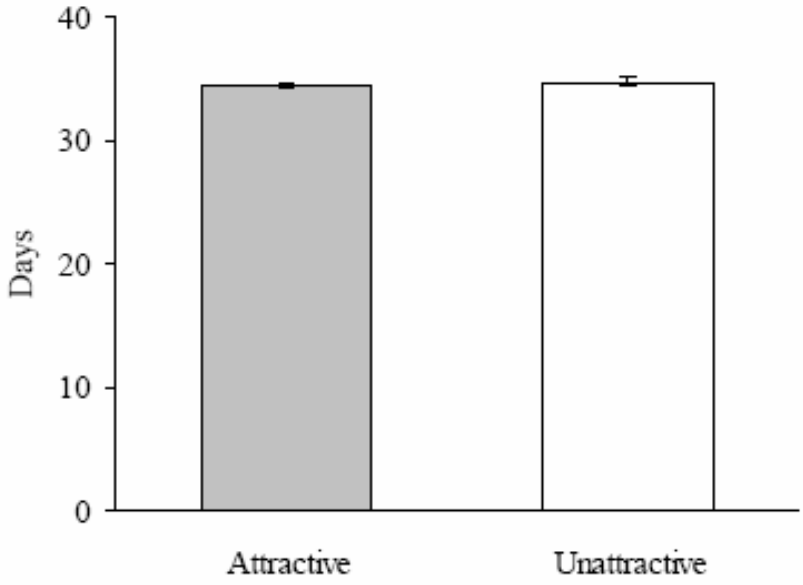

Figure 3-3. Mean (± S.E.) embryo development time (number of days between oviposition and emergence) of offspring produced by females in the attractive and unattractive groups.

Hatchling size

Hatchlings produced by females of the attractive group were significantly bigger than those produced by females of the unattractive group (Table 3-3).

Table 3-3. Comparison of five carapace dimensions (see Figure 3-1) of hatchlings produced by females in the attractive and unattractive groups.

Dimension (mm)	Attractive	Unattractive	Mann-Whitney *U* test		
			U	N_A,N_U	***p***
CL	1.03 ± 0.02	0.98 ± 0.02	17.0	10,10	0.012*
DPLE	0.48 ± 0.01	0.45 ± 0.01	14.5	10,10	0.007**
WAME	0.47 ± 0.01	0.44 ± 0.01	18.5	10,10	0.017*
WALE	0.71 ± 0.01	0.68 ± 0.01	19.0	10,10	0.019*
WPLE	0.74 ± 0.01	0.70 ± 0.01	16.0	10,10	0.010*

* indicates significance; ** indicates strong significance.

Juvenile survivorship

Juveniles produced by females of the attractive group had significantly higher survivorship than those produced by females of the unattractive group (Figure 3-4), and the difference was also significant for adults ($U = 23.0$, $p = 0.033$).

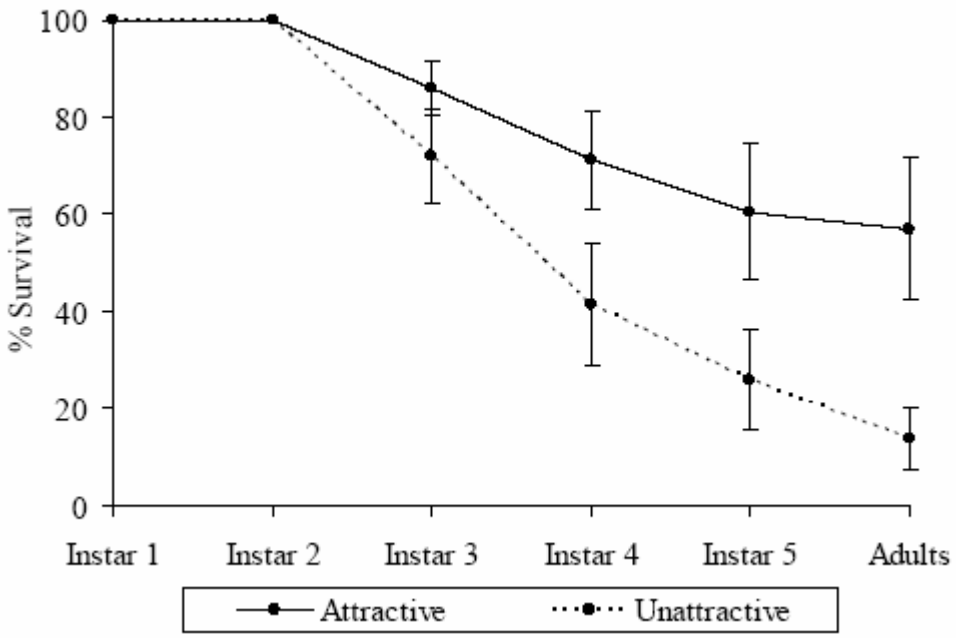

Figure 3-4. Mean (± S.E.) instar survivorship of offspring produced by females in the attractive and unattractive groups.

Juvenile development time

Juveniles produced by females of the attractive group grew faster when compared to those produced by females of the unattractive group (Figure 3-5). Female offspring from the attractive group reached adulthood earlier than those from the unattractive group (Figure 3-5a), but the difference was not significant ($U = 8.0$, $p = 0.214$). However, male offspring produced by females from the attractive group grew significantly faster and became subadults (instar 5) significant earlier than those from the unattractive group (Figure 3-5b; $U = 0$, $p = 0.036$).

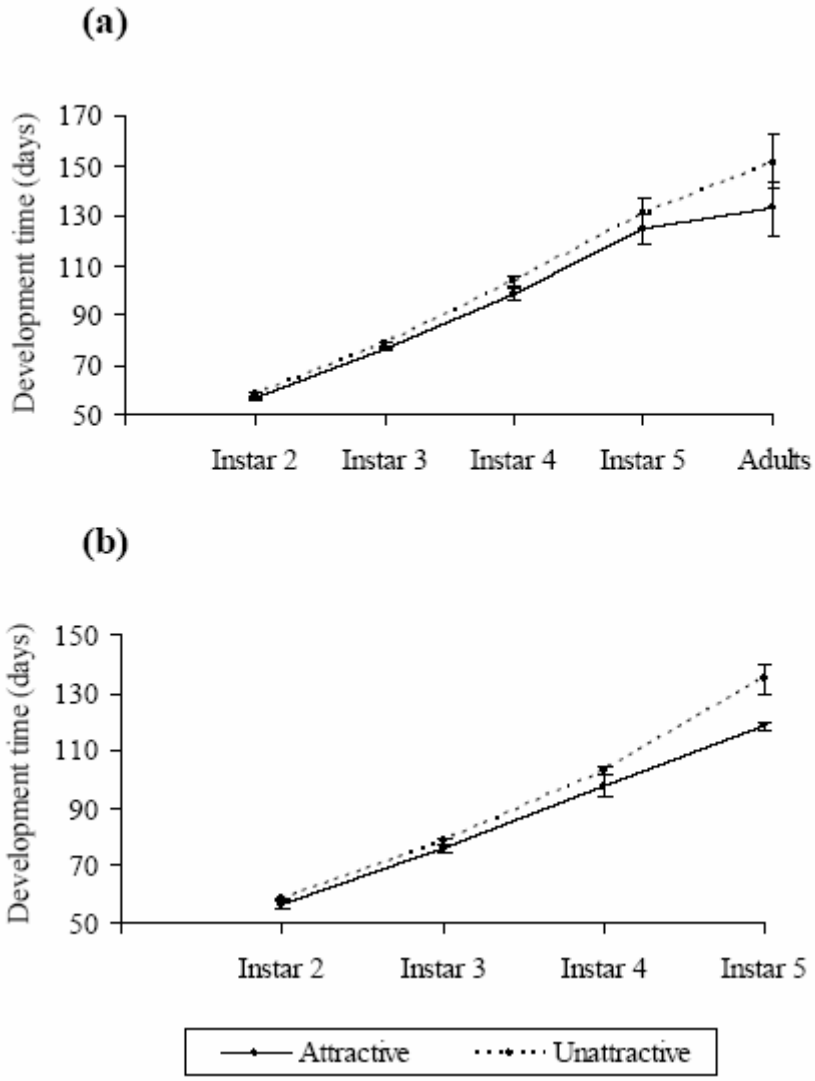

Figure 3-5. Mean (± S.E.) development time of (a) female offspring and (b) male offspring produced by females in the attractive and unattractive groups.

Juvenile size

Female offspring produced by females of the attractive group were larger than those produced by females of the unattractive group (Figure 3-6), and the differences were significant for DPLE, WAME and WALE at instar 4, and WAME at instar 5 which is the subadult stage (Table 3-4).

Similarly, male offspring produced by females of the attractive group were larger than those produced by females of the unattractive group (Figure 3-7), and the differences were significant for DPLE, WAME and WPLE at the subadult stage (Table 3-5).

Table 3-4. Female offspring carapace dimensions for instar 4, instar 5 (subadult) and adult.

Instar	Dimension (mm)	Attractive	Unattractive	Mann-Whitney *U* test		
				U	N_A, N_U	p
4	CL	1.82 ± 0.04	1.75 ± 0.03	14.5	10,5	0.198
	DPLE	0.77 ± 0.01	0.73 ± 0.01	7.0	10,5	0.027*
	WAME	0.79 ± 0.01	0.74 ± 0.01	7.0	10,5	0.027*
	WALE	1.18 ± 0.02	1.13 ± 0.02	9.0	10,5	0.049*
	WPLE	1.23 ± 0.02	1.17 ± 0.02	9.5	10,5	0.057
5	CL	2.08 ± 0.04	1.95 ± 0.04	6.0	8,4	0.089
	DPLE	0.87 ± 0.02	0.82 ± 0.02	6.0	8,4	0.089
	WAME	0.89 ± 0.02	0.83 ± 0.02	3.0	8,4	0.027*
	WALE	1.34 ± 0.03	1.26 ± 0.02	6.0	8,4	0.089
	WPLE	1.40 ± 0.03	1.31 ± 0.02	5.0	8,4	0.062
Adult	CL	2.14 ± 0.05	2.08 ± 0.05	13.5	8,4	0.671
	DPLE	0.89 ± 0.02	0.87 ± 0.02	12.0	8,4	0.496
	WAME	0.90 ± 0.01	0.90 ± 0.02	15.5	8,4	0.932
	WALE	1.37 ± 0.03	1.33 ± 0.03	10.0	8,4	0.308
	WPLE	1.43 ± 0.03	1.39 ± 0.03	12.0	8,4	0.496

* indicates significance.

Table 3-5. Male offspring carapace dimensions for instar 4 and instar 5 (subadult).

Instar	Dimension (mm)	Attractive	Unattractive	Mann-Whitney *U* test		
				U	N_A, N_U	p
4	CL	1.77 ± 0.04	1.69 ± 0.02	6.0	4,6	0.201
	DPLE	0.76 ± 0.01	0.718 ± 0.01	3.5	4,6	0.069
	WAME	0.76 ± 0.02	0.73 ± 0.01	3.5	4,6	0.069
	WALE	1.16 ± 0.02	1.11 ± 0.02	4.5	4,6	0.108
	WPLE	1.20 ± 0.02	1.14 ± 0.02	4.0	4,6	0.088
5	CL	2.10 ± 0.09	1.90 ± 0.03	1.0	3,5	0.053
	DPLE	0.88 ± 0.01	0.82 ± 0.01	0.0	3,5	0.025*
	WAME	0.88 ± 0.02	0.84 ± 0.01	0.0	3,5	0.024*
	WALE	1.34 ± 0.03	1.26 ± 0.02	1.0	3,5	0.051
	WPLE	1.39 ± 0.03	1.28 ± 0.02	0.0	3,5	0.025*

* indicates significance.

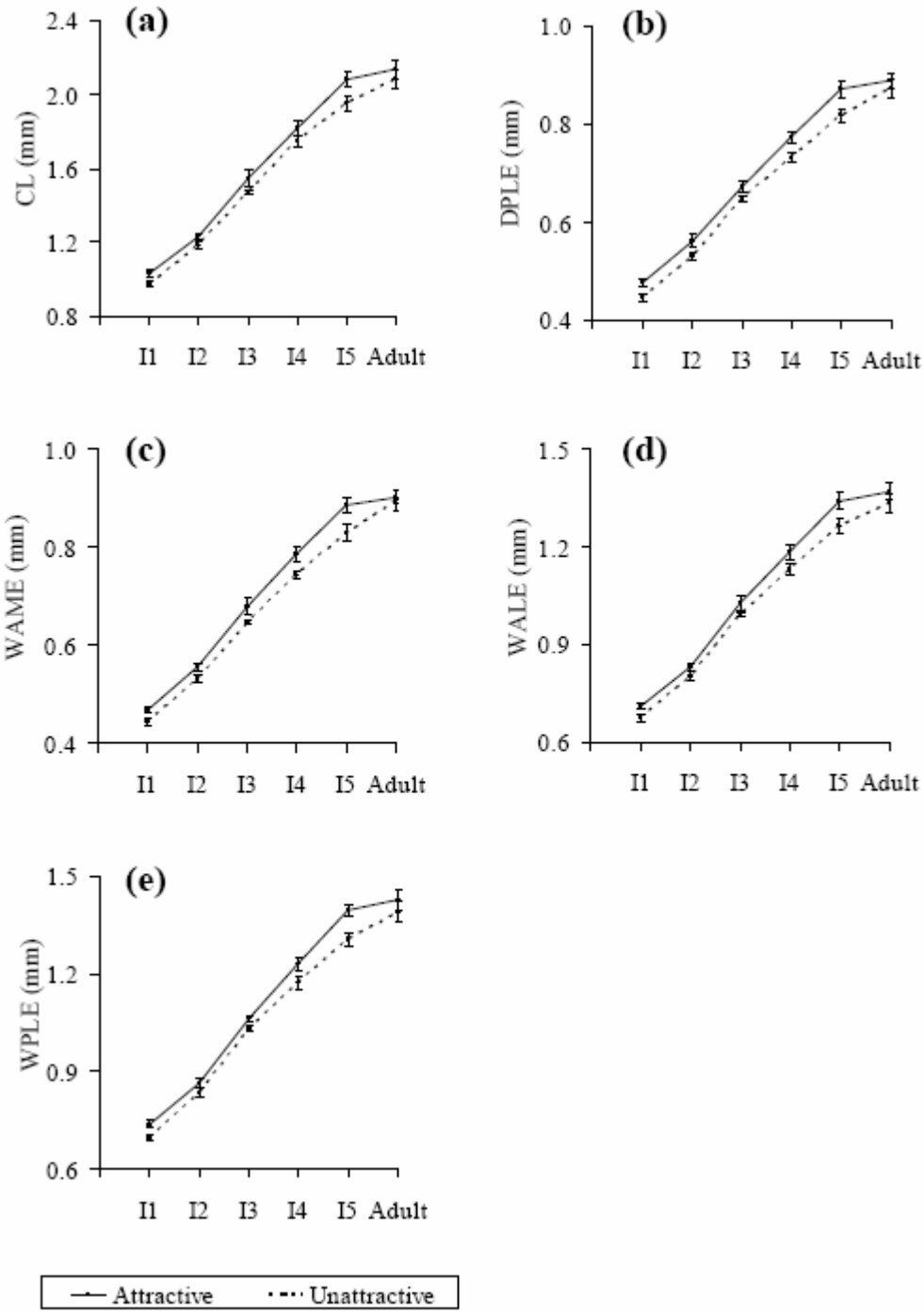

Figure 3-6. Carapace dimensions of female offspring produced by females of the attractive and unattractive groups: (a) CL; (b) DPLE; (c) WAME; (d) WALE; and (e) WPLE. Each point represents mean ± S.E.

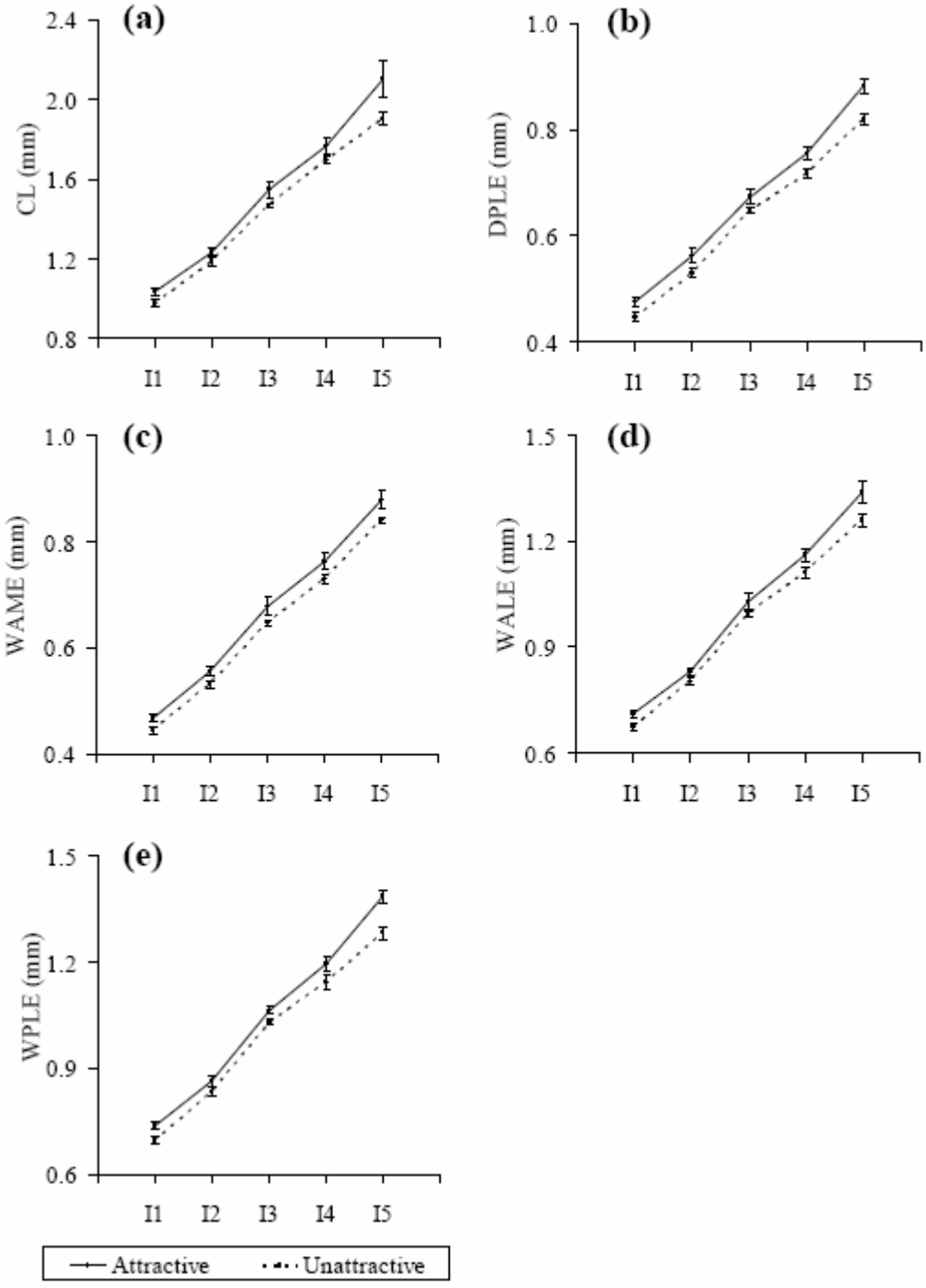

Figure 3-7. Carapace dimensions of male offspring produced by females of the attractive and unattractive groups: (a) CL; (b) DPLE; (c) WAME; (d) WALE; and (e) WPLE. Each point represents mean ± S.E.

Offspring spectral reflectance characteristics

To examine the effects of female mate choice on male offspring spectral reflectance data, Mann-Whitney *U* tests were performed to test for spectral differences between subadult male offspring of attractive and unattractive groups. Note that sample sizes were small because of the unforeseen low survivorship of male offspring at the subadult instar. Chroma was not included in the analyses of UVA-UVB reflectance spectra because they lacked a distinctive trough between the two bands (Figure 3-9) which made it unfeasible for the chroma of UVA and UVB bands to be accurately estimated (Lim & Li 2006b).

UV-VIS spectral characteristics

For the carapace spectral characteristics, subadult male offspring of the attractive group were more VIS saturated and UV brighter compared to those of the unattractive group (Table 3-6). However, there were no significant differences between male offspring of the two groups for the other spectral characteristics (Table 3-6).

When abdominal spectral characteristics were compared, no significant differences were found for any of the male offspring spectral characteristics between the attractive and unattractive groups (Table 3-6).

UVA-UVB spectral characteristics

For carapace spectral characteristics, subadult male offspring of the attractive group were UVA brighter than those in the unattractive group (Table 3-7).

However, there were no significant differences between male offspring of the two groups for the other spectral characteristics (Table 3-7).

When abdominal spectral characteristics were compared, no significant differences in UVA or UVB were found for any of the male offspring spectral characteristics between the attractive and unattractive groups (Table 3-7).

Table 3-6. Comparison of subadult male offspring UV-VIS spectral characteristics between attractive and unattractive groups.

Body part	Spectral traits	Attractive	Unattractive	Mann-Whitney U test		
				U	N_A,N_U	p
Carapace	UV Hue (nm)	396.4 ± 1.5	398.7 ± 1.8	5.0	3,6	0.302
	UV Chroma (%nm^{-1})	0.524 ± 0.004	0.36 ± 0.08	3.0	3,6	0.120
	UV Brightness (%nm)	1599.1 ± 131.6	549.6 ± 191.1	1.0	3,6	0.039*
	VIS Hue (nm)	613.6 ± 1.4	609.4 ± 3.6	3.0	3,6	0.121
	VIS Chroma (%nm^{-1})	0.495 ± 0.019	0.267 ± 0.048	0.0	3,6	0.020*
	VIS Brightness (%nm)	13964.7 ± 1286.9	8684.1 ± 1627.4	3.0	3,6	0.121
Abdomen	UV Hue (nm)	446.7 ± 0.9	443.2 ± 1.2	2.0	3,6	0.071
	UV Chroma (%nm^{-1})	0.302 ± 0.007	0.329 ± 0.028	6.0	3,6	0.435
	UV Brightness (%nm)	517.0 ± 33.9	223.3 ± 81.3	2.0	3,6	0.071
	VIS Hue (nm)	694.2 ± 3.2	673.9 ± 6.3	2.0	3,6	0.071
	VIS Chroma (%nm^{-1})	0.346 ± 0.005	0.306 ± 0.015	3.0	3,6	0.118
	VIS Brightness (%nm)	11939.4 ± 766.2	12746.6 ± 857.4	7.0	3,6	0.606

* indicates significance.

Table 3-7. Comparison of subadult male offspring UVA-UVB spectral characteristics between attractive and unattractive groups.

Body part	Spectral traits	Attractive	Unattractive	Mann-Whitney U test		
				U	N_A,N_U	p
Carapace	UVB Hue (nm)	297.7 ± 1.2	300.9 ± 0.9	2.0	3,6	0.071
	UVB Brightness (%nm)	1154.3 ± 31.4	998.7 ± 145.2	6.0	3,6	0.437
	UVA Hue (nm)	396.5 ± 0.9	399.1 ± 2.0	3.0	3,6	0.121
	UVA Brightness (%nm)	2712.7 ± 173.5	1822.9 ± 174.2	1.0	3,6	0.039*
Abdomen	UVB Hue (nm)	263.5 ± 2.4	294.3 ± 7.9	2.0	3,6	0.071
	UVB Brightness (%nm)	725.8 ± 82.7	837.8 ± 84.8	5.0	3,6	0.302
	UVA Hue (nm)	324.3 ± 2.0	391.6 ± 18.5	3.0	3,6	0.121
	UVA Brightness (%nm)	1932.1 ± 221.6	1918.8 ± 113.9	8.0	3,6	0.796

* indicates significance.

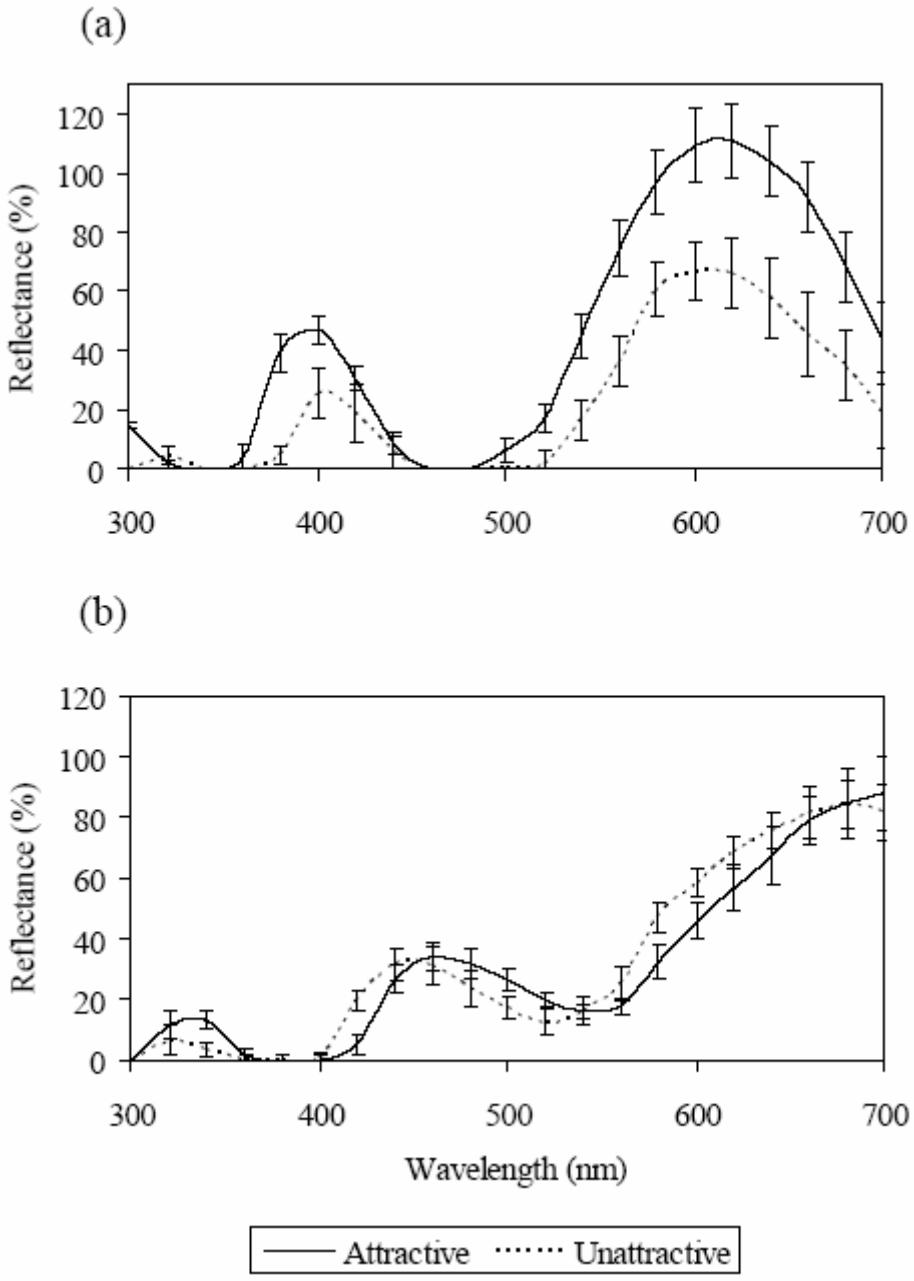

Figure 3-8. UV-VIS reflectance spectra of the (a) dorsal carapace and (b) dorsal abdomen of subadult male offspring in the attractive and unattractive groups.

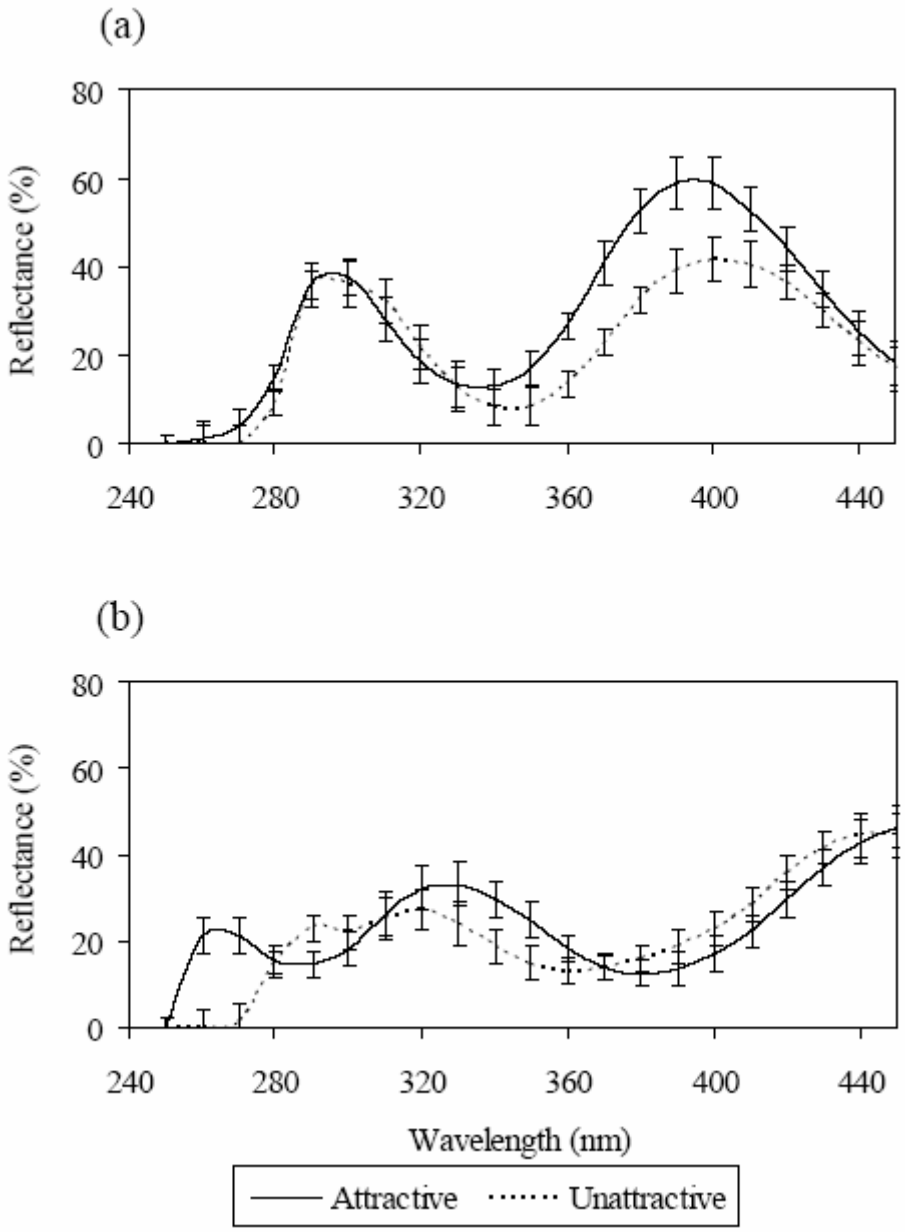

Figure 3-9. UVA-UVB reflectance spectra of the (a) dorsal carapace and (b) dorsal abdomen of subadult male offspring in the attractive and unattractive groups.

DISCUSSION

I have examined a number of direct fitness components in females, as well as a combination of fitness components in the offspring of attractive and unattractive males in this study. My results provide the first evidence that UV-based female mate-choice do not provide females any direct benefits as a consequence of their mate choice. However, this study is the first demonstration of male attractiveness being genetically associated with offspring viability, growth rate, size, as well as the attractiveness of sons. This suggests that females gain indirect genetic benefits by choosing to mate with more attractive males, thus satisfying the criteria of the good genes model. Hence, the findings provide strong empirical evidence supporting the hypothesis that UV-based female mate choice has evolved because male attractiveness is indicative of male genetic quality.

The UV-based female mate choice of *C. umbratica* has no influence on female fertility since the fertility of females that mated with preferred males was not significantly different compared to those that mated with non-preferred males. However, some studies of a variety of other animals reported contrasting results (Evans *et al.* 2010; Forstmeier & Leisler 2004; Koh *et al.* 2009; Lehtonen & Lindström 2007; Moore 1994; Petrie & Williams 1993; Reynolds & Gross 1992). Evans *et al.* (2010) reported that the Australian rainbowfish (*Melanotaenia australis*) produces almost twice as many eggs when mated with larger, preferred males compared with when they were mated with smaller non-preferred males. Forstmeier and Leisler (2004) also found that the great reed warbler (*Acrocephalus arundinaceus*) lays more eggs when mated to preferred males

compared with when mated to non-preferred males. In addition, a study on spitting spiders (*Scytodes spp.*) revealed that females lay more eggs and produce more hatchlings for attractive males, demonstrating that female mate choice influences fecundity and fertility (Koh *et al.* 2009). My results show the opposite for the salticid *C. umbratica,* perhaps because males of variable attractiveness do not differ in terms of their ability to fertilise eggs. Hence, studies should be conducted to examine the differences in ejaculate quantity or quality between attractive and unattractive males in order to further explore this possibility.

Fecundity is defined as the total number of eggs produced by a female. For spiders, it is generally calculated by counting the total number of spiderlings that hatched and the total number of unfertilised eggs, and subsequently adding the numbers together (Koh *et al.* 2009). However, fecundity data was not collected in this study because when nests were dissected to determine the number of eggs that had not hatched (i.e. unfertilized), no such eggs could be found. The reason for this is currently unknown, but it is possible that unfertilised eggs were consumed by the female.

After oviposition, the female *C. umbratica* remains inside the sealed nest until the hatchlings emerge from the nest approximately 35 days later (embryo development time). The reason for this parental care-like behaviour is unknown, but it is clearly a costly investment of time during which the female may forage, mate and produce more clutches of eggs to increase her reproductive output within her lifetime instead. The embryo development time of offspring sired by preferred males did not differ significantly from those sired by non-preferred

males, indicating that neither of the two groups of females invested more time than the other. Thus, there is no evidence that female mate choice provides direct benefits in terms of reduction in the costs of parental care.

Nevertheless, it is interesting to note that significantly more females that mated with non-preferred males were observed to consume and reabsorb their eggs. This is the first time that this behaviour was ever recorded for *C. umbratica*, thus its function still remains poorly understood. A study performed by Koh *et al.* (2009) on spitting spiders *Scytodes* spp. reported similar observations. They found that females which mated with non-preferred males had a higher tendency to consume their egg sacs before the eggs hatched. Egg-consuming behaviour shortly after oviposition may possibly serve an important function of alleviating the costs of parental care at an early stage, and will certainly be advantageous if eggs fathered by non-preferred males have low fertilisation success or simply contain inferior genes. By consuming the eggs, the female may leave the nest earlier and find another mate. Hence, future studies on *C. umbratica* should focus on this egg-consuming behaviour in order to understand its functions and consequences better.

When comparing hatchling size, it was found that hatchlings sired by preferred males were significantly larger then those sired by non-preferred males. There are two possible explanations for the difference in hatchling size between offspring of the two groups of males. The larger hatchling size of offspring sired by preferred males might have been the effect of the preferred male's good genes. Alternatively, the difference in hatchling size might have been caused by the

female's differential investment. According to the differential allocation hypothesis, females that have mated with high-quality males would increase their investment in the offspring in order to amplify the pre-existing benefits of their mate choice (Burley 1986; von Engelhardt *et al.* 2006; Sheldon 2000; Williamson *et al.* 2006). Since hatchling size is known to be influenced by the size or contents of the egg, both of which are under the control of the female, it is possible that larger hatchling size may be the result of females favouring offspring which were sired by attractive males over those which were sired by unattractive males (Sheldon 2000).

Unfortunately, it was not feasible to measure the size or weight of eggs in this study, therefore the possibility of maternal effects on hatchling size could neither be supported nor eliminated. Nevertheless, female fertility data in this study provided evidence that females which mated with preferred males did not produce more offspring than non-preferred males, hence suggesting that females did not produce more eggs in favour of preferred males. If maternal effects were present, it would be implied that females did not differentially vary the quantity of eggs, but possibly the quality of eggs instead (McCormick 1999). Conversely, if maternal effects were absent, it would be implied that the difference in hatchling size was possibly the genetic effect of males. Since size is one of the fitness components, it could also be implied that females might gain indirect benefits via increased offspring fitness when mating with attractive males. Therefore, future studies should test the differential allocation hypothesis in *C. umbratica* females in order to evaluate the above-mentioned possibilities.

Results of my study also revealed that offspring sired by preferred males had higher survivorship than offspring sired by non-preferred males. Significantly more offspring sired by attractive fathers survived to sexual maturity when compared to those sired by unattractive males. Survivorship is deemed as a major fitness component, simply because an individual's reproductive success depends on the prerequisite that the individual survives to sexual maturity (Clutton-Brock 1988; Newton 1989). Hence, most studies of good genes sexual selection have focused on this fitness component (reviewed by Møller & Alatalo 1999). My findings were consistent with many of these studies (Crocker & Day 1987; Hasselquist *et al.*1996; Norris 1993; Petrie 1994; Sheldon *et al.* 1997; Welch *et al.* 1998), hence suggesting that *C. umbratica* females do gain indirect genetic benefits as a consequence of their UV-based mate choice. This is consistent with the good genes hypothesis of sexual selection by female mate choice.

Additionally, male offspring sired by preferred males grew faster than those sired by non-preferred males. Similarly, a study conducted by Moore (1994) which provided empirical evidence that female mate choice of the cockroach (*Nauphoeta cinerea*) has indirect benefits. Female cockroaches that mated with attractive males produced offspring with shorter development times than those produced by females that mated with less preferred males.

It is somewhat puzzling but interesting to note that *C. umbratica* female mate choice had no effect on the development time of female offspring. This observation of a male-biased effect is the first to be ever recorded for this species of jumping spiders, hence future studies should focus on investigating this

interesting phenomenon. Nevertheless, my findings demonstrated that male offspring enjoyed higher fitness and benefited from their mother's mate choice because they reached reproductive age earlier, hence further supporting the view that *C. umbratica* females gain indirect genetic benefits as a consequence of their mate choice.

Males that were more attractive to females also sired offspring that were significantly larger in size than those sired by unattractive males. Such offspring thus enjoyed higher fitness because of all the advantages that come with having a larger size. For instance, larger body size has been correlated with greater female fecundity in a variety of animals including insects (Honek 1993), crustaceans (McLaren 1965), amphibians (Tilley 1968), and mammals (Sand 1996). Larger size is also generally related to higher resource holding potential which is an important factor in male-male competition (Alcock 1995; Bisazza *et al.* 1996; Forslund 2000; Kelly 2008). Male size is also commonly positively correlated with female preference (Forslund 2000; Fukaya 2004). In addition, having a larger size may allow an individual to hunt for bigger prey, and hence increasing foraging efficiency (Mittelbach 1981). Numerous studies conducted on a variety of animals also provided evidence that attractive males produce larger sized offspring, such as those done on birds (Petrie 1994), amphibians (Mitchell 1990; Welch *et al.* 1998), fish (Reynolds & Gross 1992) and insects (Iyengar & Eisner 1999).

My results also revealed that *C. umbratica* female mate choice had no effect on the size of female offspring at adulthood. Despite having larger sizes at the

juvenile and subadult stages, female offspring sired by attractive males were not larger than those sired by unattractive males at sexual maturity, and therefore did not enjoy benefits such as the capacity to produce more or larger eggs. This observation is also the first to be recorded for *C. umbratica*. Hence, further studies would be required in order to fully understand the implications of this interesting finding. Nevertheless, my findings demonstrate that for the fitness component - size, offspring of attractive males had higher fitness than offspring of unattractive males, hence further supporting the good genes hypothesis that *C. umbratica* females gain indirect genetic benefits as a consequence of their mate choice.

The analysis of male offspring spectral reflectance revealed that attractive fathers produced sons that had UV brighter and more VIS saturated (i.e., chroma) carapace than sons that were fathered by unattractive males. As revealed in the findings of Chapter 2, females tended to prefer males with higher chroma and brightness for VIS and UV wavebands. Hence, findings in the present study suggest that the sons of preferred males would be more attractive to females when compared to sons of non-preferred males. Numerous other studies also reported similar findings in guppies (*Poecilia reticulate*) (Brooks 2000), *Hyalella* amphipods (Cothran 2008), *Drosophila* spp. flies (Etges 1996; Rundle *et al.* 2007), house crickets (*Acheta domesticus*) (Head *et al.* 2005), sandflies (*Lutzomyia longipalpis*) (Jones *et al.* 1998), cockroaches (*Nauphoeta cinerea*) (Moore 1994), and field crickets (*Gryllus bimaculatus*) (Wedell & Tregenza 1999). Additionally, the results in this study revealed that the attractive trait in preferred males is heritable. Therefore, these findings provided further evidence

that supports the good genes hypothesis. Nevertheless, a limitation of this study was its small sample size which was due to the unforeseen low survivorship of male offspring at the subadult and adult stages. Hence, larger sample sizes should be used for similar studies in the future.

There is one potential confounding factor in this study which must be considered. It is possible that the higher level of fitness in offspring sired by attractive males was the result of maternal differential allocation effects rather than paternal genetic effects. As predicted by the differential allocation hypothesis, females could produce larger or better-quality eggs in response to being mated with attractive males (Cunningham & Russell 2000; Sheldon 2000). This could lead to enhanced performance of offspring, as illustrated in several studies (Benoit & Pepin 1999; Einum & Fleming 1999; Heath *et al.* 1999; Koh *et al.* 2009; McCormick 1999; Räsänen *et al.* 2005). However, such an observation has never been observed in *C. umbratica* yet. Nonetheless, differential allocation of greater reproductive effort in the offspring of attractive males is only adaptive if there is already a fitness benefit when mated to attractive males. This infers that both the good genes and Fisherian sexy son models of intersexual selection are possible explanations for the evolution of female mate choice in *C. umbratica*. Therefore, future studies should test the differential allocation hypothesis in *C. umbratica* females in order to account for this potential confounding factor.

Although the findings in this study provide empirical support for the indirect benefits models of intersexual selection, it should be noted that the good genes and Fisherian sexy son models are not mutually exclusive mechanisms. In fact,

both of them should be considered as equally possible, and might even work in partnership leading to the evolution of female mate choice in *C. umbratica*. Nevertheless, it would prove to be extremely helpful if Zahavi's handicap principle is considered. According to this principle, honest indicators of good genes are costly because only the fittest signalers can afford them (Zahavi 1975; Zahavi & Zahavi 1997). Male ornaments selected by good genes mechanism should be condition-dependent in order to honestly indicate the male's superior genes. A study conducted by Lim & Li (2007) revealed that UV reflectance in *C. umbratica* is a condition-dependent trait which is indicative of a male's feeding history. Therefore in the next chapter, I focused on investigating the honesty of male UV reflectance as an indicator of its quality.

CONCLUSION

Female preference was previously found to be related to UV brightness and chroma (Chapter 2). In this chapter, the fitness consequences of this UV-based female mate-choice were examined. No evidence was found to support the hypothesis that females receive direct benefits in terms of fertility as a result of their mate choice, but preferred males produced offspring that had higher survivorship and growth rates, and were significantly larger in size than offspring sired by non-preferred males. Females that mated with preferred males also produced more attractive sons in terms of UV reflectance. This study is the first to demonstrate that females gain indirect benefits as a result of their UV-based mate choice in *C. umbratica* specifically, and possibly in any animal in general. In order to distinguish the relative importance of the good genes and Fisherian sexy

son hypotheses in the evolution of *C. umbratica* female mate choice, the next chapter was an investigation of the reliability of male UV reflectance as an indicator of its quality.

CHAPTER 4

The Effects of Diet Quality on UV Reflectance and Fitness of the Jumping Spider *Cosmophasis umbratica*

Abstract. The handicap hypothesis of sexual selection has been a popular topic in discussions about the evolution of sexual ornaments in recent years. Many sexual-selected ornaments are known to depend on the condition of the individual that bears it. Recent studies have shown that UV reflectance is important in female mate choice and condition-dependent in a wide range of animal taxa. However, no study has determined whether UV reflectance is dependent on diet quality. In this study, I tested whether diet quality affects UV reflectance in the jumping spider *C. umbratica* by monitoring the development of *C. umbratica* juveniles reared on diets of different nutrient content. *C. umbratica* juveniles reared on the nutrient-enriched diet grew faster, were larger, and adult males were more saturated and brighter in both UV and VIS wavelengths. These findings show that *C. umbratica* male UV reflectance is dependent on the diet quality during the development. Moreover, UV reflectance is positively correlated to fitness components such as development time and juvenile size. Therefore, my results indicate that UV reflectance in *C. umbratica* may be a reliable indicator of male quality which females may use as a criterion in making mate choice decisions.

Keywords: Jumping spider, *Cosmophasis umbratica*, sexual selection, diet quality, condition-dependent.

INTRODUCTION

In recent years, the handicap hypothesis of sexual selection has been a popular topic in discussions about the evolution of sexual ornaments (Andersson 1994). It predicts that females have evolved to prefer mates with costly condition-dependent ornaments which honestly indicate male genetic quality (good genes models), because males in poorer conditions are unable to afford the viability costs (Zahavi 1975; Zahavi & Zahavi 1997).

Many sexual-selected ornaments are known to depend on the condition of the individual that bears it (Delhey *et al.* 2006; Doucet 2002; Keyser & Hill 1999, 2000; Mougeot *et al.* 2005). For example, studies have shown that condition-dependent ornaments are indicators of immunocompetence (Barber *et al.* 2001; Peters *et al.* 2004), parasite load (Mougeot *et al.* 2005), sexual maturity (Jouventin *et al*. 2005), sperm quality (Peters *et al.* 2004), reproductive status (Cuadrado 2000; Carazo *et al.* 2003; Doucet *et al*. 2005; Gaskett 2004; Ruiz *et al.* 2008; Weiss 2006), and age (Andersson & Amundsen 1997; Delhey & Kempenaers 2006; Griggio *et al.* 2003; Lim & Li 2007; Mougeot *et al.* 2005; Siefferman *et al.* 2005).

Nutrient content is known to influence male ornament development and adult attractiveness (Eraly *et al.* 2009; McGraw *et al.* 2002; Naguib & Nemitz 2007; Olhsson 2002). It is known that the dietary conditions an organism experiences during its development can have a significant effect on its performance as an adult (Birkhead *et al.* 1999; Desai & Hales 1997; Elo & Preston 1992). Nutritional level or content experienced during an individual's development may

be influenced by factors such as the quantity of prey and the nutritional quality of prey (Mayntz & Toft 2001). For example, in some birds, the reduction in the quantity or quality of food received by nestlings has been shown to influence a number of adult characteristics such as body size, probability of survival, secondary sexual traits and immune function (de Kogel 1997; Gershwin *et al.* 1985; Lochmiller *et al.* 1993; Richner *et al.* 1989). Studies on invertebrates such as wolf spiders (*Pardosa amentata*) have also found similar results (Mayntz & Toft 2001). They demonstrated that when fed with high-protein prey, wolf spiders enjoyed better survivorship and higher growth rates compared to those that were fed with low-protein prey. Another study conducted by Lim & Li (2007) revealed that UV reflectance in the jumping spider *Cosmophasis umbratica* is indicative of a male's feeding history. Well-fed males have brighter abdomens in both the UV and VIS wavelength ranges when compared to starved males. However, this study only examined the quantitative effect of food on male UV reflectance, and the qualitative effect of food remains unknown. Hence, the final part of my research focused on investigating the effects of diet quality on the fitness of *C. umbratica* in terms of its survivorship, development time, size, and UV reflectance. The hypothesis that male UV reflectance is an indicator of a male's nutritional history in *C. umbratica* was also tested.

MATERIALS AND METHODS

Spider collection and maintenance

Adult *C. umbratica* females were collected from Ulu Pandan Park Connector in Singapore during the day (particularly at 0900-1100hrs, and 1600-1800hrs) between June 2008 and June 2009. All spiders were housed individually in a plastic cylindrical cage (diameter × height: 70 × 85 mm) and maintained under controlled laboratory conditions of 25 ± 1^{o}C, relative humidity of 70 – 80%, and photoperiod of 12 hr light:12 hr dark. Additional illumination was provided from full-spectral fluorescent tubes (2% UVB, 10% UVA, 300–700 nm, 36", 30W; Arcadia Natural Sunlight Lamp, Croydon, Angleterre, UK) which simulate natural sunlight, in order to closely mimic the illumination in their natural habitat. Water and 10% sucrose solution was provided *ad libitum* through the use of dental rolls.

Experimental design and procedures

To examine whether nutrient content would affect UV reflectance of male *C. umbratica* and offspring fitness, a total of 30 females were used and monitored daily to check for the presence of eggs so as to record the date of oviposition. The egg-sacs produced by these females were then randomly assigned to two experimental groups (nutrient-enriched and control. See below). The nests were monitored daily to check for the hatching of eggs and the emergence of spiderlings from the nest. However, it was not feasible to account for the hatching date of each egg and the date of the first moult for each postembryo within the silken nest. Therefore, these data were not collected, and only the date of

oviposition and spiderling emergence were recorded. All hatchlings were separated and individually housed within 7 days upon emergence.

Hatchlings assigned to the nutrient-enriched group were reared on a diet of wild type fruit flies cultured on instant *Drosophila* medium (Formula 4-24, Plain, Carolina Biological Supply Company) added with amino acids (22090 Casein Hydrolysate, Sigma-Aldrich), with each *Drosophila* culture bottle containing 2 g of instant medium and 0.15 g of casein hydrolysate (contains all 20 natural occurring amino acids). Hatchlings assigned to the control group were reared on a diet of wild type fruit flies (*Drosophila melanogaster*) cultured on traditional banana medium. All spiders were fed three times a week, with prey provided in excess to ensure that the spiders never starved. Pilot experiments revealed that some hatchlings starved to death because they experienced difficulties capturing wild type fruit flies. In order to prevent this, newly emerged spiderlings were given vestigial (wingless) fruit flies (*D. melanogaster*) in addition to their assigned prey during their first 14 days to ensure that they capture their first meal. Spiderlings that starved to death because they failed to feed were excluded from the experiments.

To evaluate the dietary effects on the two groups of spiders, the survivorship, development time and size of all juveniles produced by females of both groups were monitored until they reached sexual maturity or died (Li & Jackson 1997). Juvenile mortality and moults were checked and recorded daily, and the exuviae were collected for size measurements. Body lengths and five carapace dimensions (Figure 4-1; Li & Jackson 1997) of exuviae were measured using an

ocular micrometer (resolution 0.01 mm) in a stereomicroscope (Leica MZ16A). Spiders that moulted to adulthood were also measured at 24 hours after moulting.

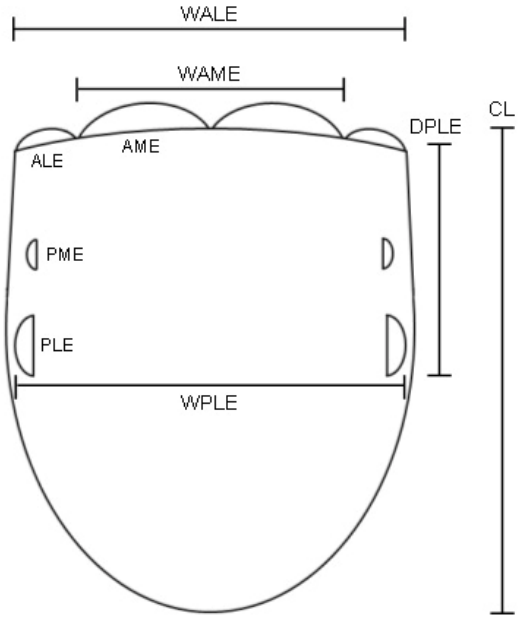

Figure 4-1. Diagram of a *Cosmophasis umbratica* carapace. ALE: anterior lateral eyes; AME: anterior median eyes; PLE: posterior lateral eyes. The bars indicate the five carapace dimensions that were measured: CL, carapace length; DPLE, distance between ALE and PLE; WAME, WALE, and WPLE, distance between the outside margins of AME, ALE, and PLE, respectively.

Spectrophotometric measurements

To examine differences in male spectral reflectance between the nutrient-enriched and control groups, spectrophotometric measurements were performed on the tenth day after the final moult of each male spider. Measurement procedures were the same as in the previous two chapters (for details, see Chapter 2). Spiders were mildly anaesthetized by carbon dioxide gas

for three minutes before measurements were performed. Reflectance in the wavelength range of 250–700 nm was measured from two body parts of every spider: dorsal carapace and dorsal abdomen. For each body part, five readings were recorded, with each reading obtained from a randomly selected position. The five readings were subsequently averaged to obtain a reflectance spectrum which was used to obtain the hue, chroma and brightness of the UV and VIS wavebands.

Data analysis

All data were tested for normality using the Kolmogorov-Smirnov tests prior to any other statistical analyses. All data were presented as mean ± S.E. All statistical tests were two-tailed and the significance level was set at $P < 0.05$ ($\alpha = 0.05$), unless otherwise stated. All tests were run using SPSS 16.0 for Windows.

Two-sample *t*-tests were performed to check that effects of maternal spider mass, size and age were controlled for the two experimental groups. For any data that was not normally distributed, Mann-Whitney *U* tests were performed instead (Zar 1999). Differences in spider survivorship, development time and size between the high-quality and low-quality groups were analysed by two-sample *t*-tests for all normally distributed data. For any data that was not normally-distributed, Mann-Whitney *U* tests were performed (Zar 1999). Mann-Whitney *U* tests were also used whenever sample sizes were small ($n < 10$).

To examine dietary effects on male spectral reflectance, Mann-Whitney *U* tests were performed to test for spectral differences of adult males between the nutrient-enriched and control groups. Chroma was not included in the analyses of UVA-UVB reflectance spectra because they lacked a distinctive trough between the two bands which made it unfeasible for the chroma of UVA and UVB bands to be accurately estimated (Lim & Li 2006b).

RESULTS

Maternal mass, size and age

There were no significant differences in maternal (Table 4-1) body mass, body length, carapace length, carapace width, abdomen length and abdomen width between the nutrient-enriched and control groups.

Table 4-1. Comparison of maternal mass, size and age between the females of nutrient-enriched and control groups.

	Nutrient-enriched (n=15)	**Control (n=15)**	**Two-sample *t*-test**		
			t	***df***	***p***
Body mass (mg)	0.166 ± 0.007	0.171 ± 0.007	-0.456	28	0.652
Body length (mm)	6.58 ± 0.09	6.75 ± 0.09	-1.387	28	0.176
Carapace length (mm)	2.32 ± 0.02	2.35 ± 0.01	-1.004	28	0.324
Carapace width (mm)	1.55 ± 0.01	1.55 ± 0.01	-0.167	28	0.868
Abdomen length (mm)	4.25 ± 0.09	4.40 ± 0.09	-1.179	28	0.248
Abdomen width (mm)	2.62 ± 0.06	2.68 ± 0.05	-0.748	28	0.460

Juvenile survivorship

There were no significant differences in juvenile survivorship between the nutrient-enriched and control groups (Figure 4-2, Table 4-2).

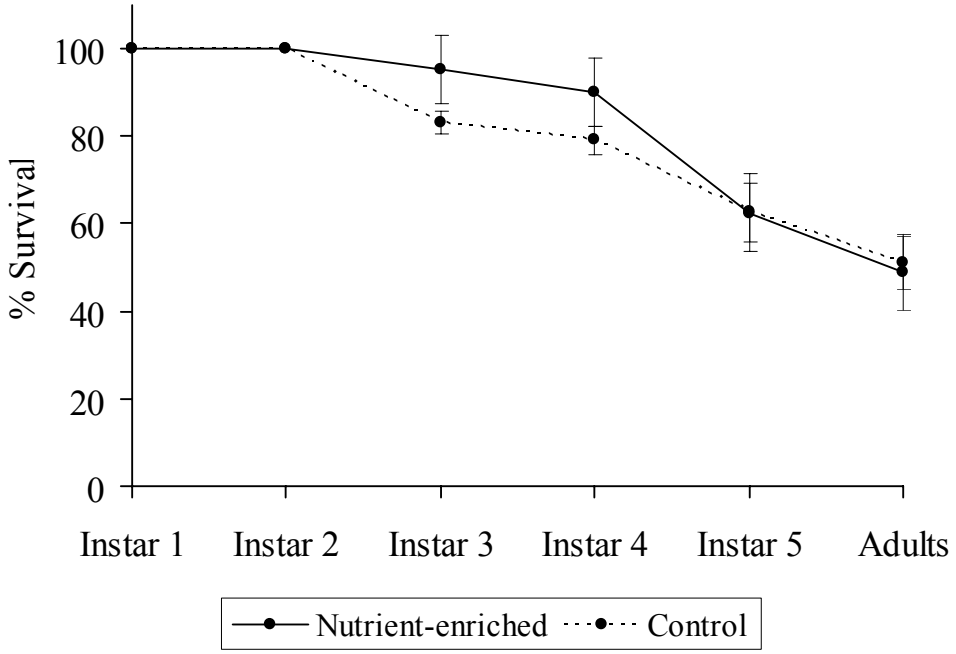

Figure 4-2. Mean (± S.E.) juvenile survivorship (%) in the nutrient-enriched and control groups.

Table 4-2. Results for the comparison of juvenile survivorship in the nutrient-enriched and control groups. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Instar 2	Instar 3	Instar 4	Instar 5	Adults
$U = 97.5$	$U = 86.0$	$U = 90.0$	$t = 0.027$	$t = 0.197$
N_E,N_C = 15,15	N_E,N_C = 15,14	N_E,N_C = 15,14	$df = 26$	$df = 26$
$p = 1.000$	$p = 0.523$	$p = 0.707$	$p = 0.978$	$p = 0.845$

Development time

Juveniles were observed to reach sexual maturity at either the 5th or 6th instar. Juveniles that were fed on the nutrient-enriched diet developed faster than those on the control diet (Figure 4-3).

Female juveniles from the nutrient-enriched diet group reached the 4th and 5th instars significantly earlier than those from the control diet group. Female juveniles on the nutrient-enriched diet also reached maturity at the 5th instar significantly earlier (Table 4-3). However, differences in development time for the male juveniles were not statistically significant (Table 4-4).

Table 4-3. Statistical test results for the comparison of female juvenile developmental time in the nutrient-enriched and control groups. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Instar 4	Instar 5	Instar 5 Adult	Instar 6 Adult
$t = 2.467$	$t = 2.817$	$U = 21.0$	$U = 30.0$
$df = 27$	$df = 25$	N_E,N_C = 10,9	N_E,N_C = 12,8
$p = 0.020$*	$p = 0.009$**	$p = 0.049$*	$p = 0.165$

* indicates significance; ** indicates strong significance.

Table 4-4. Statistical test results for the comparison of male juvenile developmental time in the nutrient-enriched and control groups. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Instar 4	Instar 5	Instar 5 Adult	Instar 6 Adult
$U = 52.0$	$U = 35.0$	$U = 5.0$	$U = 2.0$
N_E,N_C = 14,9	N_E,N_C = 11,8	N_E,N_C = 5,3	N_E,N_C = 3,2
$p = 0.488$	$p = 0.457$	$p = 0.453$	$p = 0.543$

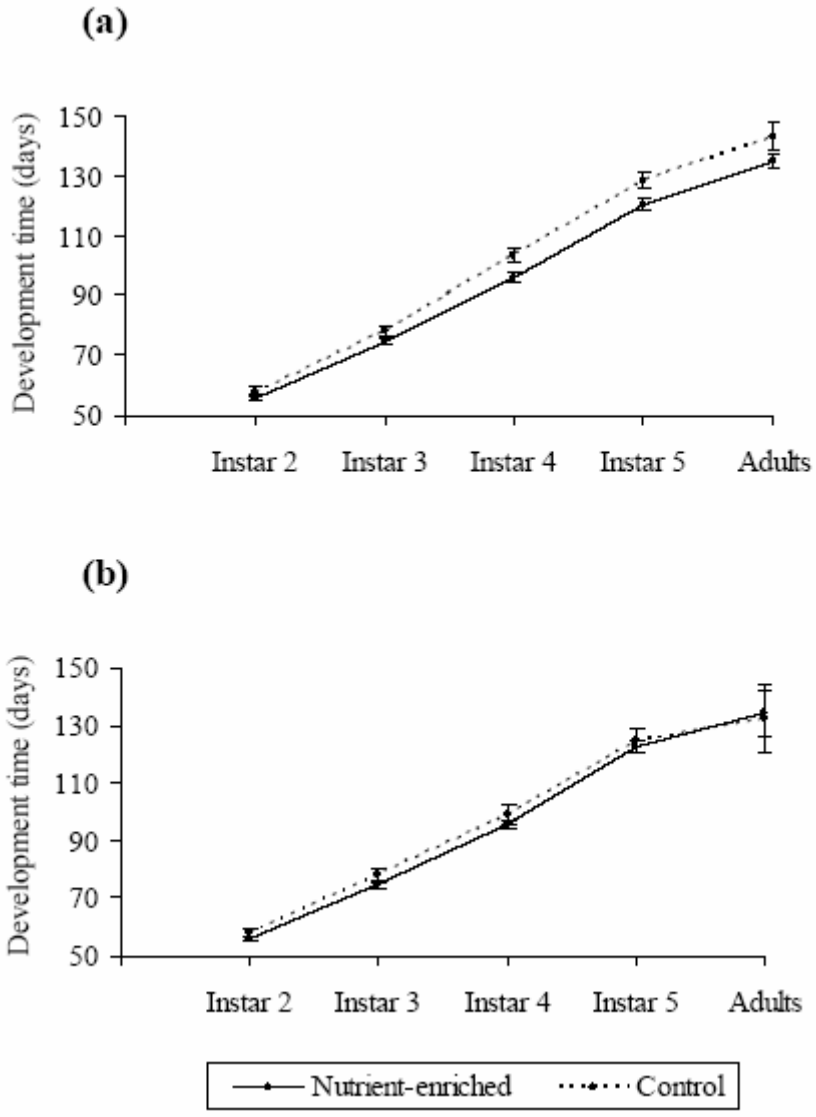

Figure 4-3. Mean (± S.E.) development time (days) of (a) female juveniles and (b) male juveniles which were fed on the nutrient-enriched diet and those which were fed on the control diet.

Spider size

At the start of the experiment, hatchlings (instar 1) from both treatment groups did not differ significantly in size (Table 4-5). However, when they subsequently moulted to the 2nd and 3rd instars, juveniles that were fed on the nutrient-enriched diet were found to be larger than those on the control diet. The differences were significant for all five carapace dimensions at instar 2, and CL, DPLE and WAME at instar 3 (Table 4-5).

Female spiders that were fed on the nutrient-enriched diet were significantly larger than those on the control diet at the 4th instar, subadult stage (instar 5), and adult stage (Figure 4-4). Significant differences were found for all five carapace dimensions at instar 4, DPLE, WAME and WALE at instar 5, and for DPLE and WALE at the adult stage (Table 4-6). Therefore, females fed on the nutrient-enriched diet were significantly larger at all life stages when compared to those on the control diet.

Similarly, male spiders that were fed on the nutrient-enriched diet were larger than those fed on the control diet (Figure 4-5). The differences were significant for all five carapace dimensions at instar 4, and for DPLE at the adult stage (Table 4-7).

Table 4-5. Juvenile carapace dimensions for the 1st, 2nd and 3rd instars.

Instar	Dimension (mm)	Nutrient-enriched	Control	Two-sample *t*-test		
				t	***df***	***p***
1	CL	0.97 ± 0.01	0.96 ± 0.01	0.692	28	0.494
	DPLE	0.44 ± 0.01	0.43 ± 0.01	0.668	28	0.510
	WAME	0.43 ± 0.01	0.43 ± 0.01	0.605	28	0.550
	WALE	0.67 ± 0.01	0.67 ± 0.01	0.811	28	0.424
	WPLE	0.69 ± 0.01	0.69 ± 0.01	0.824	28	0.417
2	CL	1.21 ± 0.01	1.17 ± 0.01	2.313	28	0.028*
	DPLE	0.54 ± 0.01	0.51 ± 0.01	3.918	28	0.001**
	WAME	0.54 ± 0.01	0.51 ± 0.01	5.260	28	<0.001**
	WALE	0.82 ± 0.01	0.79 ± 0.01	2.643	28	0.013*
	WPLE	0.85 ± 0.01	0.83 ± 0.01	2.575	28	0.016*
3	CL	1.49 ± 0.01	1.41 ± 0.03	2.814	17	0.012*
	DPLE	0.65 ± 0.01	0.62 ± 0.01	2.465	18	0.024*
	WAME	0.65 ± 0.01	0.62 ± 0.01	3.938	27	0.001*
	WALE	0.10 ± 0.01	0.97 ± 0.01	1.926	27	0.065
	WPLE	1.04 ± 0.01	1.01 ± 0.01	1.800	27	0.083

* indicates significance; ** indicates strong significance.

Table 4-6. Female spider carapace dimensions for instar 4, instar 5 (subadult) and adult instar.

Instar	Dimension (mm)	Nutrient-enriched	Control	Two-sample *t*-test		
				t	***df***	***p***
4	CL	1.81 ± 0.01	1.67 ± 0.05	3.010	14.8	0.009**
	DPLE	0.77 ± 0.01	0.71 ± 0.01	4.785	15.7	<0.001**
	WAME	0.76 ± 0.01	0.69 ± 0.01	6.268	17.4	<0.001**
	WALE	1.16 ± 0.01	1.11 ± 0.02	3.244	15.7	0.005**
	WPLE	1.21 ± 0.01	1.16 ± 0.02	2.855	15.9	0.012*
5	CL	2.10 ± 0.02	1.98 ± 0.06	1.948	8.1	0.087
	DPLE	0.86 ± 0.01	0.82 ± 0.02	3.142	18.0	0.006**
	WAME	0.87 ± 0.01	0.81 ± 0.02	3.927	18.0	0.001**
	WALE	1.33 ± 0.01	1.26 ± 0.03	2.603	18.0	0.018*
	WPLE	1.38 ± 0.01	1.33 ± 0.03	1.941	18.0	0.068
Adult	CL	2.24 ± 0.04	2.13 ± 0.05	1.995	25.0	0.057
	DPLE	0.91 ± 0.01	0.88 ± 0.01	2.246	25.0	0.034*
	WAME	0.92 ± 0.02	0.88 ± 0.01	1.699	25.0	0.102
	WALE	1.41 ± 0.02	1.36 ± 0.02	2.063	25.0	0.049*
	WPLE	1.47 ± 0.02	1.42 ± 0.03	1.604	25.0	0.121

* indicates significance; ** indicates strong significance.

Table 4-7. Male spider carapace dimensions for instar 4, instar 5 (subadult) and adult instar. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Instar	Dimension (mm)	Nutrient-enriched	Control	Mann-Whitney *U* test		
				U	N_E,N_C	***p***
4	CL	1.83 ± 0.02	1.77 ± 0.03	30.5	14,9	0.040*
	DPLE	0.78 ± 0.01	0.74 ± 0.01	21.5	14,9	0.009**
	WAME	0.78 ± 0.01	0.72 ± 0.01	13.5	14,9	0.002**
	WALE	1.19 ± 0.01	1.15 ± 0.02	30.0	14,9	0.037*
	WPLE	1.23 ± 0.01	1.19 ± 0.02	28.0	14,9	0.027*
5	CL	2.10 ± 0.03	2.07 ± 0.05	38.5	10,8	0.894
	DPLE	0.87 ± 0.01	0.85 ± 0.01	27.0	10,8	0.246
	WAME	0.88 ± 0.01	0.85 ± 0.01	24.0	10,8	0.153
	WALE	1.33 ± 0.02	1.32 ± 0.02	35.0	10,8	0.656
	WPLE	1.37 ± 0.02	1.37 ± 0.02	39.0	10,8	0.929
Adult	CL	2.15 ± 0.05	2.28 ± 0.08	5.0	6,3	0.302
	DPLE	0.87 ± 0.01	0.92 ± 0.02	1.0	6,3	0.038*
	WAME	0.86 ± 0.02	0.91 ± 0.02	3.5	6,3	0.154
	WALE	1.37 ± 0.03	1.41 ± 0.03	5.5	6,3	0.364
	WPLE	1.39 ± 0.02	1.45 ± 0.03	5.0	6,3	0.300

* indicates significance; ** indicates strong significance.

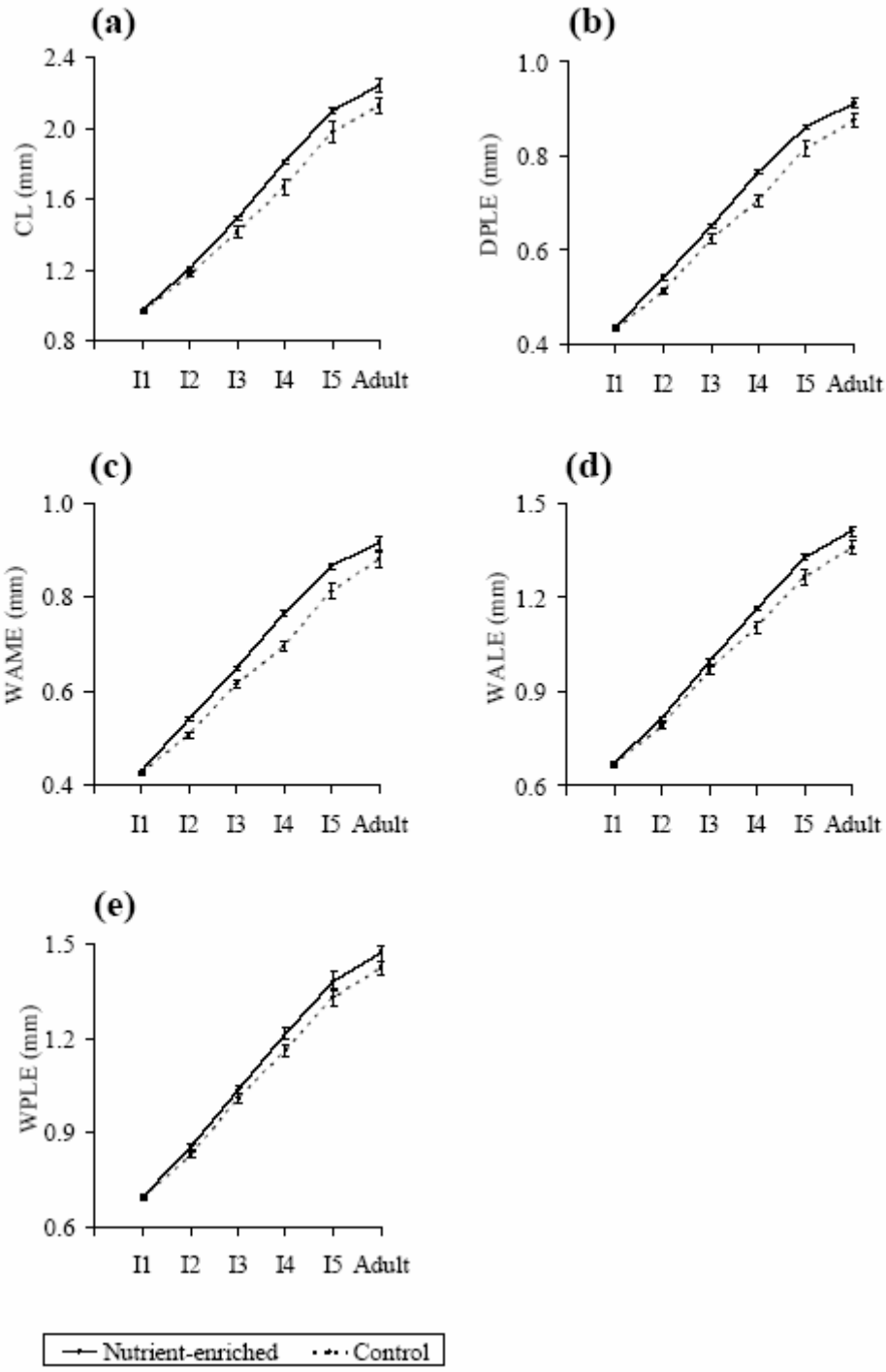

Figure 4-4. Carapace dimensions of female spiders that were reared on the nutrient-enriched and control diets: (a) CL; (b) DPLE; (c) WAME; (d) WALE; and (e) WPLE. Each point represents mean ± S.E.

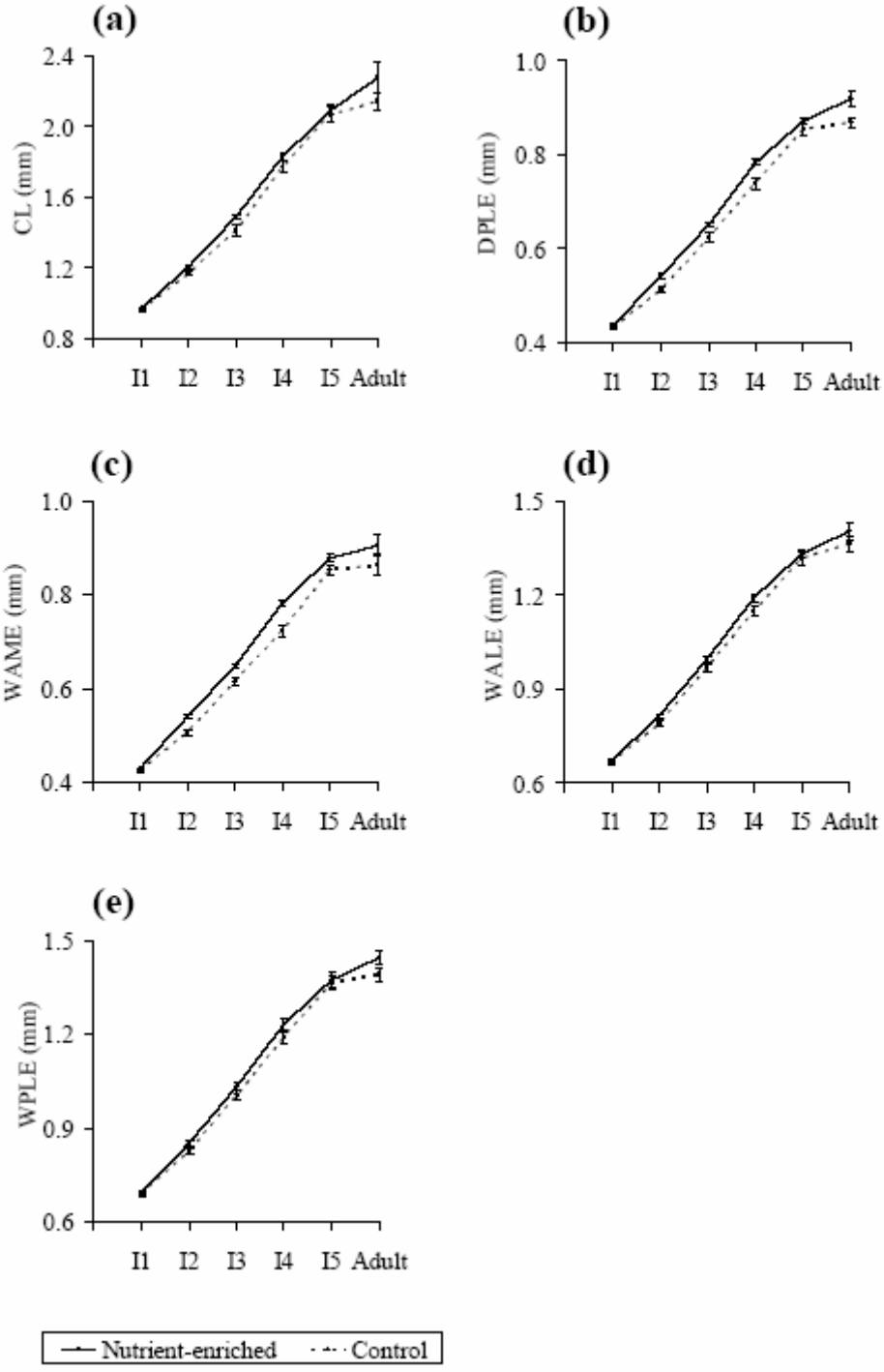

Figure 4-5. Carapace dimensions of male spiders that were reared on the nutrient-enriched and control diets: (a) CL; (b) DPLE; (c) WAME; (d) WALE; and (e) WPLE. Each point represents mean ± S.E.

Spectral reflectance characteristics

UV-VIS spectral characteristics

For the carapace spectral characteristics, UV chroma, VIS chroma, UV brightness and VIS brightness were significantly higher in male spiders that were fed on nutrient-enriched diet compared to those on the control diet (Table 4-8). There were no significant differences between male spiders of the two groups for the other spectral characteristics (Table 4-8). When abdominal spectral characteristics were compared, no significant differences were found for any of the male spectral characteristics between the nutrient-enriched and control groups (Table 4-8).

UVA-UVB spectral characteristics

For the carapace spectral characteristics, males that were fed on the nutrient-enriched diet were UVA and UVB brighter than those on the control diet (Table 4-9). When abdominal spectral characteristics were compared, UVA brightness was significantly higher in male spiders that were fed on the nutrient-enriched diet compared to those fed on the control diet. No significant differences in UVA and UVB hue as well as UVB brightness were found between the two groups of males (Table 4-9).

Table 4-8. Comparison of male UV-VIS spectral characteristics between nutrient-enriched and control groups. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Body part	Spectral traits	Nutrient-enriched	Control	Mann-Whitney *U* test		
				U	N_E,N_C	***p***
Carapace	UV Hue (nm)	386.3 ± 2.0	380.1 ± 1.2	3.0	6,3	0.121
	UV Chroma (%nm^{-1})	0.61 ± 0.04	0.42 ± 0.01	0.0	6,3	0.020*
	UV Brightness (%nm)	2498.2 ± 326.2	1084.3 ± 41.2	0.0	6,3	0.020*
	VIS Hue (nm)	599.2 ± 2.9	589.9 ± 1.6	4.0	6,3	0.197
	VIS Chroma (%nm^{-1})	0.40 ± 0.02	0.30 ± 0.01	0.0	6,3	0.019*
	VIS Brightness (%nm)	12439.3 ± 914.3	7600.0 ± 380.8	0.0	6,3	0.020*
Abdomen	UV Hue (nm)	379.5 ± 2.9	387.1 ± 2.3	3.0	6,3	0.121
	UV Chroma (%nm^{-1})	0.40 ± 0.01	0.34 ± 0.04	6.0	6,3	0.437
	UV Brightness (%nm)	1971.2 ± 123.9	1254.2 ± 224.1	2.0	6,3	0.071
	VIS Hue (nm)	606.0 ± 2.4	617.3 ± 3.2	3.0	6,3	0.121
	VIS Chroma (%nm^{-1})	0.35 ± 0.00	0.33 ± 0.03	6.5	6,3	0.508
	VIS Brightness (%nm)	17501.7 ± 395.2	16389.6 ± 2192.4	6.0	6,3	0.439

* indicates significance.

Table 4-9. Comparison of male UVA-UVB spectral characteristics between nutrient-enriched and control groups. N_E,N_C indicates the sample sizes of nutrient-enriched and control groups respectively.

Body part	Spectral traits	Nutrient-enriched	Control	Mann-Whitney U test		
				U	N_E,N_C	p
Carapace	UVB Hue (nm)	291.3 ± 1.2	287.4 ± 1.0	4.0	6,3	0.197
	UVB Brightness (%nm)	976.5 ± 82.3	612.6 ± 60.8	1.0	6,3	0.039*
	UVA Hue (nm)	387.2 ± 1.8	378.5 ± 1.1	2.0	6,3	0.071
	UVA Brightness (%nm)	3271.5 ± 237.0	2328.1 ± 44.1	0.0	6,3	0.020*
Abdomen	UVB Hue (nm)	284.1 ± 2.8	292.2 ± 0.3	5.0	6,3	0.302
	UVB Brightness (%nm)	620.7 ± 49.6	673.7 ± 3.3	9.0	6,3	1.000
	UVA Hue (nm)	380.3 ± 3.2	382.4 ± 4.8	8.0	6,3	0.796
	UVA Brightness (%nm)	3263.0 ± 123.2	2420.5 ± 222.4	1.0	6,3	0.039*

* indicates significance.

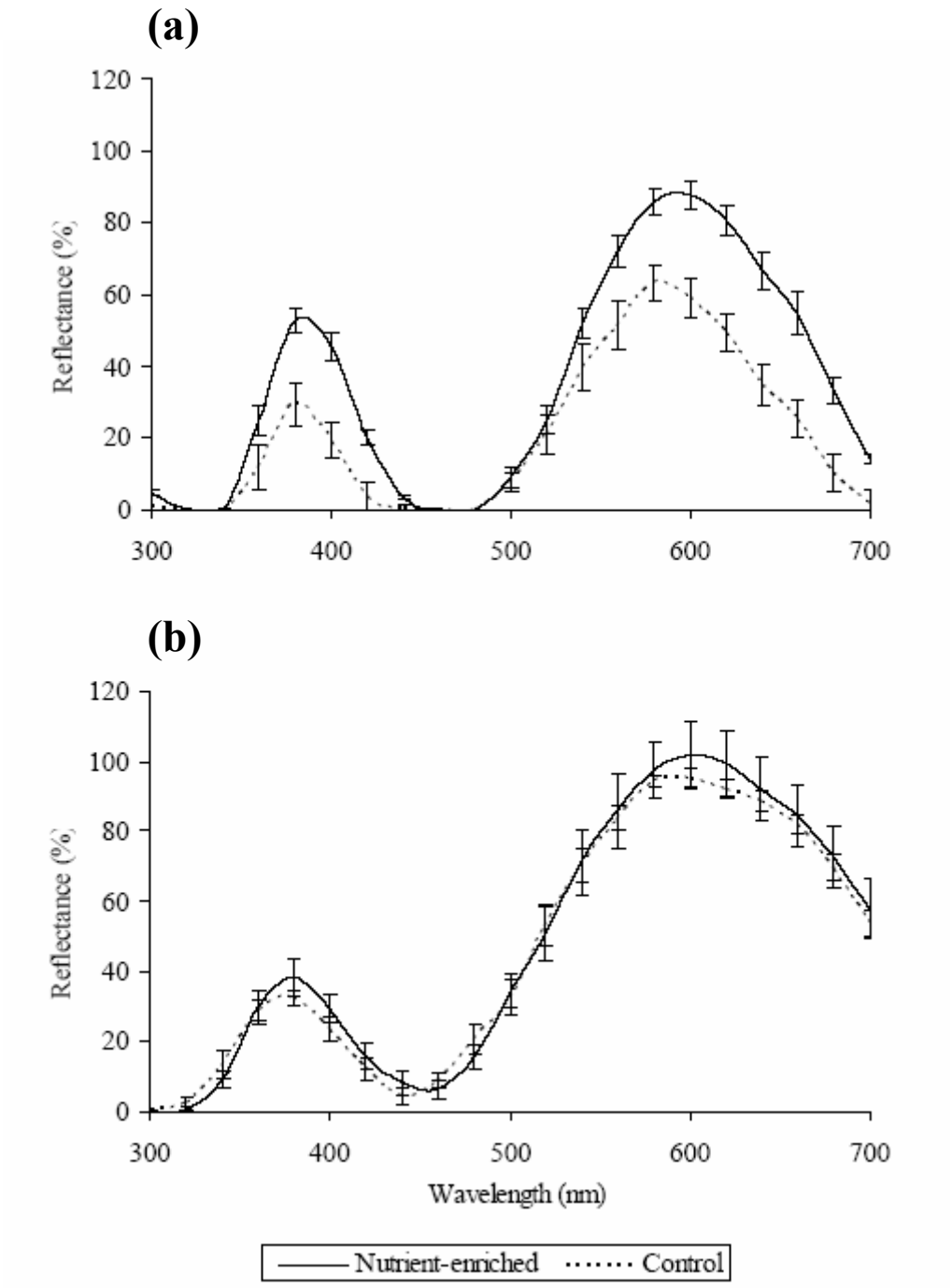

Figure 4-6. UV-VIS reflectance spectra of the (a) dorsal carapace and (b) dorsal abdomen of male spiders in nutrient-enriched and control groups.

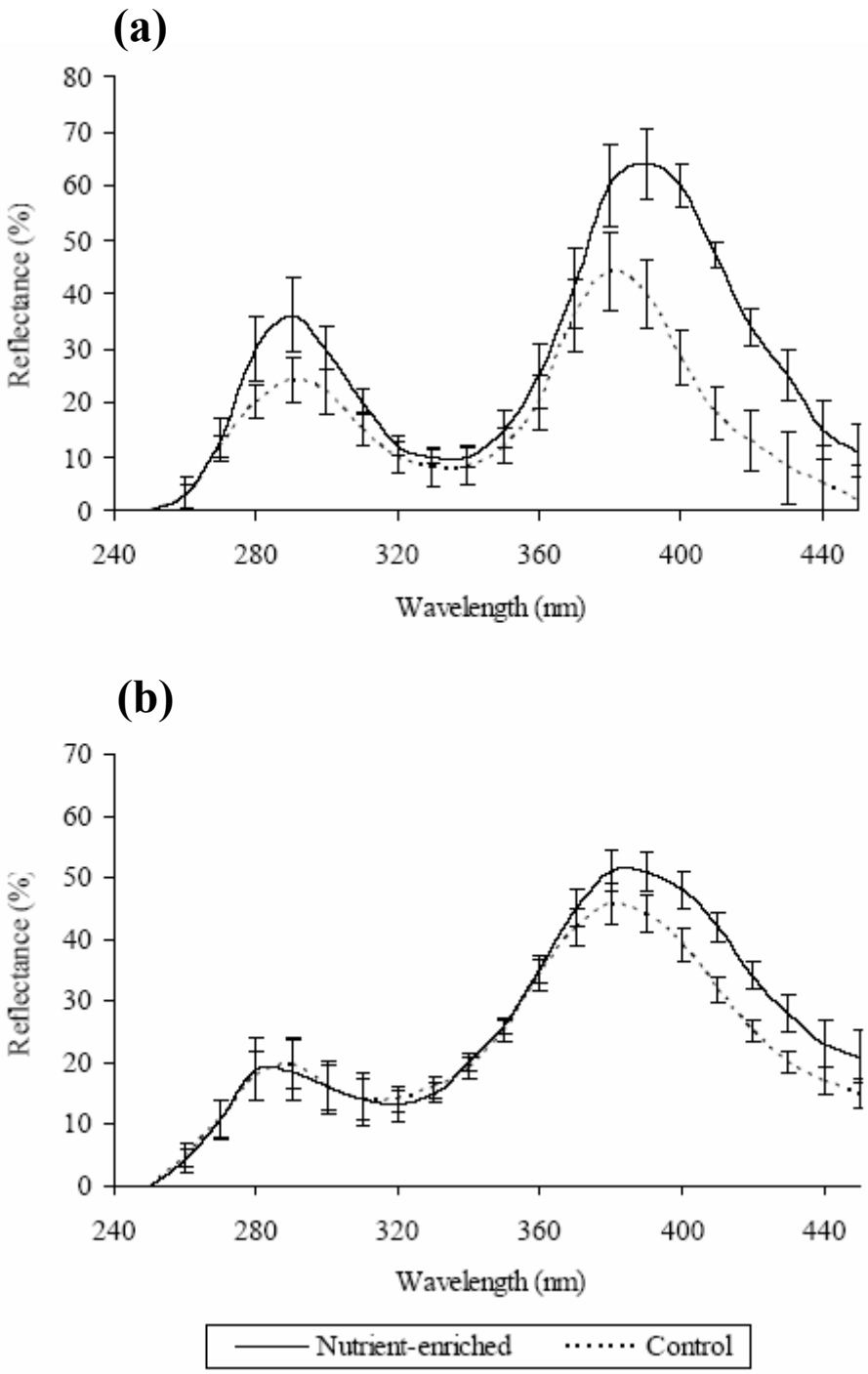

Figure 4-7. UVA-UVB reflectance spectra of the (a) dorsal carapace and (b) dorsal abdomen of male spiders in nutrient-enriched and control groups.

DISCUSSION

According to Zahavi's handicap hypothesis, male ornaments that are costly to produce are accurate measures of male quality because only better-conditioned individuals can afford the costs (Cotton *et al.* 2004; Zahavi 1975; Zahavi & Zahavi 1997). Hence, female mate choice evolves because females gain indirect genetic benefits via producing offspring with enhanced fitness. This is consistent with the good genes hypothesis of intersexual selection. In Chapter 3, I showed that *C. umbratica* females gain indirect genetic benefits as a result of their UV-based mate choice. In this chapter, my findings provide strong evidence that UV reflectance in *C. umbratica* is dependent on the diet's nutrient content or quality during juvenile development, and diet quality is closely related to the fitness of *C. umbratica*. This indicates that UV reflectance in *C. umbratica* may be a reliable indicator of male nutritional history and quality.

Diet quality was found to have no effect on juvenile survivorship in *C. umbratica*. A similar result has been reported for zebra finches where differences in diet quality had no effect on the survivorship (Boag 1987). However, some studies on wolf spiders (*Pardosa amentata* and *Lycosa helluo*) show contrasting results (Mayntz & Toft 2001; Uetz *et al.* 1992). Wolf spiders fed with fruit flies reared on culture medium supplemented with amino acids enjoyed higher survivorship when compared to those that were fed with fruit flies reared on plain culture medium (Mayntz & Toft 2001). It is possible that the differences in nutritional composition between the two diets used in this study were unable to affect the spiders' ability to survive under laboratory conditions. Future studies of dietary

effects on *C. umbratica* survivorship should use a larger number of diet treatment groups with varying nutritional quality.

Diet quality had an obvious effect on *Cosmphasis umbratica* juvenile growth rate. Juveniles that were reared on the nutrient-enriched diet grew faster than those reared on the control diet. Similar findings have also been reported for wolf spiders (Uetz *et al.* 1992). Wolf spiders (*Lycosa helluo*) that were reared on a diet consisting of many prey types have shorter development times than those fed with only one prey type (Uetz *et al.* 1992). Another study which examined dietary effects on zebra finch development also reported that zebra finches reared on a supplemented diet show a higher rate of development when compared to those reared on a basic diet (Birkhead *et al.* 1999). *C. umbratica* that feed on nutrient-enriched prey enjoy shorter development times, and hence benefit because they contribute their genes to future generations more rapidly (Cooch *et al*. 2002) and may have access to more potential mates (Vollrath & Parker 1992). Interestingly, results in this study suggest that diet quality only has significant effects on female growth rate but not on male growth rate in *C. umbratica*. A possible explanation for this sex-specific growth rate is that males from both diet groups might have been developing at a suppressed rate. Males may require certain nutrients for their development which females do not, and the concentration of such nutrients might be low in the fruit flies of both diet groups. Hence, future studies should attempt to identify the essential nutritional components for the development of *C. umbratica* males.

My findings indicated that nutrient content also influences *C. umbratica* juvenile body size. Juveniles that were reared on the nutrient-enriched diet were larger. In a similar study, Uetz *et al.* (1992) found that wolf spiders (*Lycosa helluo*) that were reared on a high quality diet were larger in size than spiders that were reared on a low quality diet. Boag (1987) also reported that zebra finches reared on a higher quality diet are larger compared to those reared on a lower quality diet. Size is commonly used as a measure of fitness, because having a larger size is often related to better foraging efficiency and predator defense (Mittelbach 1981). Body size has also been shown to be positively correlated with resource holding potential which is an important factor in male-male competition (Alcock 1995; Bisazza *et al.* 1996; Forslund 2000; Jackson & Cooper 1991; Kelly 2008; Whitehouse 1991), female preference (Forslund 2000; Fukaya 2004), and female fecundity in a variety of animals including insects (Honek 1993), crustaceans (McLaren 1965), amphibians (Tilley 1968), and mammals (Sand 1996). Hence, larger body size can be translated as higher level of fitness. Nevertheless, the findings in this study indicate that diet quality is positively related to the fitness of *C. umbratica*.

My results also provide evidence that nutrient content affects UV reflectance of male offspring in *C. umbratica*. Male offspring that were reared on the nutrient-enriched diet had higher carapace chroma and brightness for both UV and VIS wavebands when compared to those which were reared on the control diet. Males that were reared on the nutrient-enriched diet also had UVA and UVB brighter carapaces. Similarly, the UV reflectance of male ornaments has also been demonstrated to be affected by nutritional condition in another study

conducted by Keyser and Hill (1999) in which they found that the plumage UV reflectance of blue grosbeaks (*Guiraca caerulea*) is positively correlated with nutritional condition.

Interestingly, my results reveal no differences in any of the abdomen spectral characteristics between males of the two diet groups. This suggests that carapace spectral characteristics may be relatively more important as indicators of diet quality compared to abdomen spectral characteristics. In contrast, Lim and Li (2007) reported that hunger level or nutrient quantity strongly affects the abdomen UV reflectance of *C. umbratica* but not carapace UV reflectance. These indicate that UV reflectance of different body parts may carry different information, and each may separately act as an indicator of male quality component such as hunger level or nutritional condition.

The nutritional quality of an individual's diet has significant effects on its viability and reproductive success. High nutritional quality of the diet has been shown to be associated with earlier maturation, larger size and better condition in a range of animals (Geister *et al.* 2008; Naya *et al.* 2007; Uetz *et al*. 2002). Additionally, several studies have revealed that differences in nutrient content of the diet have important effects on male ornament development and adult attractiveness (Eraly *et al.* 2009; Geister *et al.* 2008; Kotiaho 2000; McGraw *et al.* 2002; Naguib & Nemitz 2007; Olhsson 2002). For example, in the wolf spider *Schizocosa ocreata*, body conditions and sexual ornaments were shown to be dependent on prey type (Uetz *et al.* 2002), hence providing support for the view

that nutritional quality of the diet can affect an individual's condition and attractiveness to potential mates.

CONCLUSION

The results from Chapter 3 provide evidence that *C. umbratica* females gain indirect genetic benefits as a result of their UV-based mate-choice. In this chapter, my findings show that UV reflectance of the male ornament is influenced by diet quality during development in *C. umbratica*. Moreover, UV reflectance is positively related to fitness components such as development time and size. Therefore, these findings indicate that UV reflectance in *C. umbratica* may be a reliable indicator of male quality by which females use as a criterion in making mate-choice decisions.

CHAPTER 5

General Discussion

The purpose of this study was to investigate UV-based female mate choice and its ultimate causes in the jumping spider *C. umbratica*. The findings from this thesis provide strong evidence that UV reflectance of *C. umbratica* is a sexually selected trait which may serve as an indicator of male quality to females in order to help them make adaptive mate choice decisions. More importantly, my study demonstrates for the first time that UV-based female mate choice provides not direct but indirect genetic benefits to females mating with preferred males that are UV brighter.

UV reflectance as an honest indicator of good genes

The findings in this thesis suggest that UV-based female mate choice in *C. umbratica* evolved because UV reflectance is a reliable indicator of male quality in terms of his genes and nutritional condition. The good genes model of sexual selection predicts a correlation between female mate choice and offspring fitness (Andersson 1994; Hamilton & Zuk 1982; Lande 1981; Zahavi 1975). Indeed, my findings show that *C. umbratica* offspring sired by preferred males have higher fitness. Numerous other studies also provided empirical support for the good genes model. For example, Welch *et al.* (1998) evaluated the benefits of preferring long-duration calls in female gray tree frogs (*Hyla versicolor*) by comparing the fitness of maternal half-siblings sired by males with different call durations. They found that the offspring of preferred males showed better

performance during larval and juvenile stages than the offspring of non-preferred males. Norris (1993) also reported similar findings from his study on great tits (*Paus major*). He investigated the viability of offspring fathered by males of varying attractiveness and found that offspring fitness is positively correlated to the attractiveness of their fathers. Hence, female mate choice in *C. umbratica* might have evolved because of the indirect benefits which females gain from mating with males of good genetic quality.

Furthermore, UV reflectance in *C. umbratica* is condition-dependent, and is indicative of the nutritional quality of the male's diet. Additional support for the good genes model also comes from the evidence that variations in nutrient composition of the diet bear fitness costs. My findings suggest that when spiders experience low nutritional conditions during their development, they have low fitness and are unable to afford the production costs of UV-reflecting ornaments that are attractive to females. In contrast, spiders that are able to acquire higher nutrient levels during their development may have better body conditions and fitness, and thus are able to produce attractive UV-reflecting ornaments. Therefore, it may be predicted that spiders of variable genetic quality differ in their foraging efficiency in the wild, and thus experience variable nutritional conditions which in turn determine their capacity to produce costly but attractive ornaments. According to Zahavi's handicap principle, honest indicators of superior genes are costly because only the fittest individuals can afford them (Johnstone 1995; Zahavi 1975; Zahavi & Zahavi 1997). Hence, *C. umbratica* females gain indirect genetic benefits through enhanced offspring fitness when

they base their mate choice decisions on UV-reflecting ornaments which accurately signify male genetic quality.

Ultimate causes of UV-based female mate choice

Both the good genes and Fisherian sexy son mechanisms may have roles in the evolution of UV-based female mate choice in *C. umbratica*. The findings in this thesis provide strong support for the existence of indirect genetic benefits to female mate choice (good genes model), but they cannot be interpreted as providing negative evidence for the Fisherian sexy son mechanisms of sexual selection. The good genes model and Fisherian sexy son model are not opposing theories of sexual selection. In fact, it is possible for Fisherian sexy son mechanisms to work in concert with any other mechanisms of mate choice evolution (Jones & Ratterman 2009). Fisher proposed that a genetic covariance between the male trait and the female preference allows the male trait to be maintained because such males produce sons that are attractive or "sexy" and daughters that prefer such a trait (Fisher 1915, 1930). Three processes are involved: initial preference of a male trait, self-reinforcing process of female preference and male trait elaboration, and the end of elaboration due to reproductive benefits being counterbalanced by survival costs of natural selection (Fisher 1915, 1930; Jones & Ratterman 2009). Indeed, my findings demonstrated that females that mate with attractive males produce attractive sons, which support the Fisherian sexy son hypothesis as well.

Limitations

Small sample sizes

In Chapter 3 where the fitness consequences of female mate choice were examined, I compared the development of offspring sired by ten attractive males and ten unattractive males. These sample sizes were quite small, particularly at subsequent instars due to unanticipated high mortality rates of offspring especially for those fathered by unattractive males. When evaluating the spectral differences of sons sired by attractive and unattractive fathers, data from subadult males was used for comparisons instead of data from adults. This was because of the unforeseen high mortality rates of offspring which resulted in extremely small sample sizes of males that survived till adulthood, particularly in the unattractive group. In Chapter 4 where the dietary effects on UV reflectance and fitness were investigated, I compared the development of spiders between two groups - offspring from 15 females reared on nutrient-enriched diet versus offspring from 15 females reared on control diet. Although the sample sizes here were larger than in Chapter 3, and sufficient male adults were obtained to analyse their spectral reflectance differences, the power of statistical tests remained weak. However, due to the lengthy duration of development from eggs to adulthood in *C. umbratica* (average is 168.4 days, longest recorded is 185 days), I was unable to collect larger sample sizes within the timeframe of my M.Sc. candidature. Hence, it would be good if future replica studies expand the sample sizes of data collected in order to augment the power of data analyses.

Possibility of maternal effects on offspring fitness

I have demonstrated that offspring of attractive males enjoy higher fitness because they inherited their fathers' good genes, but maternal effects may contribute to a certain degree as well. Unfortunately, my study is unable to clearly distinguish between the two. Numerous studies have demonstrated that females can increase their reproductive investment if they acquire mates of high quality. For instance, Petrie and Williams (1993) reported that peahens (*Pavo cristatus*) increase the quantity of eggs laid when mated to attractive males. Evans and colleagues (2010) also reported that female rainbowfish (*Melanotaenia australis*) increase egg deposition in favor of attractive males. These observations are consistent with the differential allocation hypothesis (Burley 1986; Sheldon 2000). This hypothesis predicts that females should differentially allocate their resources in favour of attractive males so as to amplify the benefits which are gained from mating with such males (Burley 1986; Kotiaho et al. 2003; Sheldon 2000). Females may invest differentially by varying clutch size (Galeotti *et al.* 2006; Parker 2003; Petrie & Williams 1993; Rintamäki *et al.* 1995; Thornhill 1983), egg size or mass (Cunningham & Russell 2000; Gilbert *et al.* 2006; Kolm 2001), or egg content such as nutrients, hormones or yolk antibodies (Gil *et al.* 1999, 2004; Saino *et al.* 2002). Such maternal manipulations could lead to enhanced performance of offspring, as illustrated in several studies (Benoit & Pepin 1999; Einum & Fleming 1999; Heath *et al.* 1999; Koh *et al.* 2009; McCormick 1999; Räsänen *et al.* 2005). Räsänen and colleagues (2005) investigated the effects of increased maternal investment in the moor frog (*Rana arvalis*), and found that larger eggs produced larger hatchlings which enjoyed higher fitness. Another study which evaluated the effects of maternal hormones

on larval quality of the damselfish (*Pomacentrus amboinensis*) revealed that post-fertilization exposure of eggs to cortisol or testosterone from the mother directly affects larval morphology at hatching (McCormick 1999).

In a study of red junglefowl (*Gallus gallus*) conducted by Parker (2003), he was able to distinguish between the roles of paternal and maternal effects on offspring performance. Parker performed a series of mate choice trials as well as artificial insemination experiments, and reported that higher offspring fitness sired by attractive males is exclusively caused by paternal effects (good genes) rather than maternal effects (differential investment). Currently, no studies have been performed to investigate the existence of differential allocation behaviour in *C. umbratica* females. Hence future studies should be conducted to examine this interesting behaviour in order to understand the relative roles of paternal and maternal effects in causing higher fitness in offspring sired by attractive males.

Future directions

Multiple traits as cues of female mate choice

Most studies of female mate choice have only focused on the effects of a single male trait. However, some females are known to use multiple traits when choosing mates (Head *et al.* 2005; Iwasa & Pomiankowski 1994; Møller & Pomiankowski 1993; Pomiankowski & Iwasa 1993). As such, they may be integrating information from several male traits in order to help them make mate choice decisions. Møller and Pomiankowski (1993) suggested that in some bird species, multiple traits might have evolved via Fisher mechanisms because no

evidence of condition-dependence was found. Reinforcing this view, mate preferences in multiple-ornamented bird species are believed to be weaker than in single-ornaments species (Møller 1993). However, Iwasa and Pomiankowski (1994) suggested that at least one trait among the multiple-ornamented species is a reliable indicator of male quality which had evolved via good genes mechanisms. Unfortunately, we currently have a very poor understanding of the role of multiple male traits in female mate choice. Therefore, future studies should examine the importance of multiple male traits in influencing the mate choice of females in order to achieve a better understanding of their evolution in jumping spiders.

Direct and indirect benefits

Among the large body of literature currently accumulated which focused on the evolution of female mate choice, most studies have focused on the indirect benefits of female mate choice (Lopuch & Radwan 2009; Moore 1994; Pomiankowski 1988; Punzalan *et al.* 2008), and not many studies have considered both the direct and indirect benefits of female mate choice (Cothran 2008; Head *et al.* 2005; Iyengar & Eisner 1999; Jones *et al.* 1998). Cothran (2008) showed that in *Hyalella* amphipods, females receive indirect benefits in the form of more attractive sons when mated with attractive males. In addition, they discovered that direct benefits were also gained in the form of reduced predation risk, illustrating that direct selection may also be involved in the evolution of female mate choice. Hence, future studies should be designed to empirically examine both direct and indirect benefits in order to understand their relative

importance in determining the evolution of UV-based female mate choice in *C. umbratica*, and mate choice in other animal species in general.

Costs of female mate choice

Costs incurred as a result of mate choice may potentially alter the net benefits gained by females, and affect the evolution of mating behavior and ornaments (Head *et al.* 2005). Yet empirical studies of female mate choice that considers both costs and benefits are rare (Karino *et al.* 2006; Pomiankowski 1987; Reynolds & Gross 1990). Karino and collegues (2006) found that female guppies (*Poecilia reticulata*) gain indirect benefits as a result of their mate choice because when mated with attractive males possessing long tails, females produced sons of higher attractiveness when compared to sons of unattractive males. However, they also discovered that females also incur costs in terms of lower reproductive output, and smaller sized daughters with low reproductive output as a result of their mate choice. Hence, it is crucial that both benefits and costs are considered when studies of mate choice are conducted in order to "see the bigger picture" of mate choice consequences. Moreover, data regarding mate choice costs from well-designed studies are limited at the moment (Cothran 2008; Karino *et al.* 2006; Pomiankowski 1987; Reynolds & Gross 1990). Therefore, it is important that future studies examine the costs of UV-based female mate choice in jumping spiders in comparison to the benefits.

Effects of mate choice on offspring success

In Chapter 3 of my study, I demonstrated that females gain indirect benefits when mating with attractive males by showing that the offspring fathered by preferred males bear attractive UV-reflecting ornaments. However, it would provide more convincing evidence for indirect benefits of female mate choice if I had taken a step further to measure the offspring's mating success. For instance, Cothran (2008) provided evidence that the sons of preferred male *Hyalella* amphipods enjoyed higher mating success when compared to sons of non-preferred males. Wedell and Tregenza (1999) also examined the mating success of the sons of successful male field crickets (*Gryllus bimaculatus*) and found that such sons obtain significantly more copulations than sons of unsuccessful males. In addition, Reynolds and Gross (1992) measured the reproductive output of daughters and found that daughters of attractive male guppies (*Poecilia reticulate*) have higher reproductive output when compared to the daughters of unattractive males. Hence, it would be even better if multigenerational effects of mate choice on the fitness of both sons and daughters are examined. For example, some measures such as the lifetime fecundity and fertility of daughters, as well as the lifetime reproductive output of sons (Moore 1994; Reynolds & Gross 1992) should be recorded. Such studies could provide stronger evidence for the hypothesis that female mate choice evolved as a result of the indirect benefits gained when mating with males that bear preferred traits.

Variations in female preference

Research in the evolution of male sexual ornaments has been neglecting the possibility that variations in female mate preference may exist. Sexual selection is a co-evolutionary process between males and females, therefore such a variation in female mate preference may present significant consequences for ornament evolution. Female mate preference is expected to be stronger when costs are lower, and vice versa (Cotton *et al.* 2006). Hence, variations in female preference occur because higher quality females can better afford the costs of mate choice than lower quality females, indicating that the strength of preference may be condition dependent. Cotton *et al.* (2006) presented strong evidence that female mate preferences are indeed condition-dependent. They showed that high quality females display the strongest mate preference when compared to lower quality females.

Female preferences may also be context-dependent. For example, the strength of female preferences may be influenced by local sex ratios and population density (Jennions & Petrie 1997), availability of males (Bateson & Healy 2005) and predator abundance (Godin & Briggs 1996). Godin and Briggs (1996) investigated the effect of predation risk on female preference in guppies (*Poecilia reticulata*), and found that females reduced their preference for attractive males when the risk of predation was increased. Variation in environmental factors such as physical environmental heterogeneity (e.g. ambient light or sound levels) (Jennions & Petrie 1997), and seasonality (Qvarnström *et al.* 2000) may also influence the strength of mate preference. Variation in social context and environmental factors often affect males as well, and they may alter their

behaviour, distribution, or ornament phenotypes in response (Cotton *et al.* 2006). Therefore, variations in mate preference are important possibilities to consider when sexual selection studies are conducted.

Post-copulatory sexual selection

It is known that sexual selection can operate even after copulation has occurred (Eberhard 2009). The post-copulatory equivalents of male-male competition and female choice are sperm competition and cryptic female choice respectively (Eberhard 1996; Parker 1970). Sperm competition is defined as the competition between the sperm from two or more males for the fertilization of a given set of ova (Parker 1970). This is done through the direct action by one male or his semen on the sperm of another male (Birkhead & Møller 1997; Eberhard 2009). Males of several animal species are known to use various methods to do so, such as diluting the sperm from previous males with their own ejaculate (Gage & Baker 1991) or displacing sperm from previous males (Gack & Peschke 1994; Simmons 2001; Waage 1979). Males may also employ defensive strategies such as guarding the female, physically plugging her genitalia, or inducing non-receptive behavior in her (Eberhard 2009). In cryptic female choice, females determine which male's sperm will get to fertilise her eggs, and they may do it in many ways (Birkhead 1998). An example is by discarding sperm from previous males without their knowledge (Eberhard 2009). However, such post-copulatory mechanisms of sexual selection are not well studied in jumping spiders. Therefore it would be interesting that future studies attempt to examine the relative importance of such mechanisms in the evolution of UV-reflecting ornaments in *C. umbratica* and other animals.

Other mechanisms of mate choice evolution

Other than the good genes and Fisherian sexy son mechanisms, there are other possible explanations for the evolution of UV-based female mate choice in *C. umbratica* which should not be ignored. For example, the sensory exploitation model predicts that *C. umbratica* females show a preference simply because they are predisposed to do so. Note that sensory exploitation could also work in tandem with the Fisherian sexy son mechanisms, in which its role is to establish an initial preference for a male trait which the Fisherian processes can work on. There is also the genetic compatibility model which suggests that females prefer to mate with males that are genetically compatible with them (Neff & Pitcher 2005; Ryan & Altmann 2001; Tregenza & Wedell 2000; Zeh & Zeh 1996), and the model of sexual conflict which involves antagonistic seduction and resistance between the two sexes (Cameron *et al.* 2003; Holland & Rice 1998; Maan & Taborsky 2008; Parker 2006). Very little is known about the role of these models in the evolution of UV-based female mate choice in *C. umbratica*, but all of them present extremely promising grounds for future work. Hence, it would be of interest to evaluate the relative contributions of each different model in the evolution of mate choice.

Effects in the wild

Many studies of sexual selection are based on laboratory experiments. As such, findings from these studies may be rendered irrelevant in the wild (Møller & Alatalo 1999). Fitness effects revealed in the laboratory may possibly be diminished or absent in the natural environment. Similarly, viability differences in the wild may also be absent in artificial settings in the laboratory. For instance,

natural causes of death such as predation or disease are very likely to be different between the natural and laboratory environments. As a result, findings from laboratory-based studies may not accurately reflect effects in the test subject's natural environment. Møller (1994) conducted a field study to study the fitness consequences of female mate choice in barn swallows (*Hirundo rustica*). He monitored the longevity of offspring fathered by attractive males and unattractive males and found that offspring longevity is positively correlated to the father's attractiveness. As barn swallows are known to be subjected to parasite infestations (Møller 1994), he postulated that the enhanced viability of offspring fathered by attractive males has a genetic basis, and is possibly accounted by parasite resistance. Such a study is an illustration of the importance of accounting for natural mortality causes which may otherwise be absent in laboratory-based studies. Therefore, future research of UV-based sexual selection should involve both laboratory and field studies in order to provide more definitive findings.

OVERALL CONCLUSIONS

The findings in this thesis provide strong empirical evidence that UV reflectance of the jumping spider *C. umbratica* is a sexually selected trait which plays an important role in female mate choice. Females prefer males which have higher UV chroma and brightness on the carapace and abdomen, hence suggesting that such spectral characteristics are determinants of a male's mating success in this salticid species. Attractive males were shown to confer higher fitness on their offspring. Hence for the first time, this thesis demonstrates that female *C. umbratica* spiders gain indirect genetic benefits as a result of their mate choice.

Moreover, I have revealed that UV reflectance is dependent on nutrient contents, suggesting that UV-based female mate choice in *C. umbratica* has evolved because UV reflectance is an indicator of male quality in terms of his genes and nutritional condition. Future research should examine the roles of other sexual selection mechanisms, and factors such as differential parental investment, and mate preference variations, in the evolution of UV-reflecting ornaments in *C. umbratica*. Furthermore, studies should include the effects of multiple male traits and both costs and benefits (direct and indirect) of mate preference on the mating success of offspring under laboratory and field conditions. On the whole, there seems to be extremely promising grounds for future research on UV-based sexual selection in *C. umbratica* and other salticids.

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